CAMBRIDGE UNIVERSITY PRESS
C. F. CLAY, MANAGER
LONDON : FETTER LANE, E.C. 4

LONDON : H. K. LEWIS AND CO., LTD.,
136, Gower Street, W.C. 1
LONDON : WILLIAM WESLEY AND SON,
28, Essex Street, Strand, W.C. 2
NEW YORK : G. P. PUTNAM'S SONS
BOMBAY, CALCUTTA, MADRAS : MACMILLAN AND CO., LTD.
TORONTO : J. M. DENT AND SONS, LTD.
TOKYO: MARUZEN-KABUSHIKI-KAISHA

PALÆONTOLOGY

INVERTEBRATE

BY

HENRY WOODS, M.A., F.R.S.

UNIVERSITY LECTURER IN PALÆOZOOLOGY, CAMBRIDGE.

FIFTH EDITION

CAMBRIDGE:
AT THE UNIVERSITY PRESS
1919

First Edition 1893
Second Edition 1896
Third Edition 1902
Fourth Edition 1909
Fifth Edition 1919

PREFACE TO FIFTH EDITION

THE general plan of this work is to give, in each group of the Invertebrata, first, a short account of its general zoological features with a more detailed description of the hard parts of the animals; secondly, its classification and the characters of the important genera, with remarks on the affinities of some forms; and thirdly, a description of the present distribution, and the geological range. The account of each genus is followed by the enumeration of one or more typical species, so as to guide the student in making use of a large collection.

The illustrations are employed mainly for the purpose of explaining structure and terminology, and will not enable the student to dispense with the use of specimens. The list of palæontological works is intended to indicate where further information may be obtained in any branch of the subject; it includes works of general interest in each group, and others dealing especially with British fossils.

Some new figures have been added in this edition, and the work has been revised throughout. I am indebted to Dr W. K. Spencer for much assistance in the part dealing with the Asterozoa; to Dr F. A. Bather for emendations in the account of the Pelmatozoa; to Dr W. D. Lang for help with the Polyzoa, and to other friends for various suggestions.

H. WOODS.

August, 1919.

CONTENTS

DIVISIONS OF THE BRITISH STRATIFIED ROCKS

Cainozoic or Tertiary

PLEISTOCENE	Post-glacial deposits (river-gravels, cave-deposits, etc.)
	Glacial deposits (Boulder Clay, etc.)
PLIOCENE	Forest Bed Series
	Norwich Crag Series
	Red Crag
	Coralline Crag
MIOCENE (not found in England)	
OLIGOCENE	Hamstead Beds
	Bembridge Beds
	Headon Beds
EOCENE	Bagshot, Barton, and Bracklesham Beds
	London Clay
	Oldhaven Beds
	Woolwich and Reading Beds
	Thanet Sands

Mesozoic or Secondary

CRETACEOUS	Upper	Chalk	
		Gault and Upper Greensand	
	Lower	Lower Greensand	
		Wealden	
JURASSIC	Upper	Purbeckian	
		Portlandian	
		Kimeridgian	
		Corallian	
		Oxfordian (with Kellaways Rock)	
	Middle	Great Oolite Series (Bathonian)	Cornbrash
			Forest Marble
			Bradford Clay
			Great Oolite
			Stonesfield Slate
		Inferior Oolite Series (Bajocian)	Fuller's Earth
			Inferior Oolite
			Passage beds (sands)
	Lower	Lias	

Triassic		Rhætic Series
		Keuper Series
		Muschelkalk (not found in England)
		Bunter Series

Palæozoic or Primary

Permian		Magnesian Limestone Series
		Sandstones, etc.
Carboniferous	Upper	Coal Measures
		Millstone Grit
	Lower	Carboniferous Limestone Group
Devonian and Old Red Sandstone	Upper	
	Middle	
	Lower	
Silurian	Downtonian Series	Downton Sandstone
		Upper Ludlow Beds
		Aymestry Limestone
		Leintwardine Flags
	Salopian Series	Lower Ludlow Beds
		Wenlock Limestone
		Wenlock Shale
		Woolhope Beds
	Valentian Series	Tarannon Shales
		Llandovery Beds
Ordovician		Bala or Caradoc Series
		Llandeilo Series
		Arenig Series
Cambrian	Upper	Tremadoc Slates
		Lingula Flags
	Middle	Menevian Beds
		Solva Beds (upper part of Harlech Beds)
	Lower	*Olenellus* Beds

INTRODUCTION

From the earliest times it has been known that bodies resembling marine animals occur embedded in the rocks. For several centuries two distinct views were held respecting their nature. By some persons they were thought to have once formed parts of living animals, and consequently to indicate that the spot where they are now found was in past ages covered by the sea. Others, feeling it difficult to account for so much geographical change as would be necessitated by this view, considered that they were not of organic origin at all, but had been formed by some 'plastic force' within the earth—that they were in fact 'Sports of Nature.' Since, however, these bodies resemble in every essential respect the hard parts of animals now existing, we may at once reject this hypothesis.

The remains of animals and plants of past ages preserved in the rocks are known as fossils, the study of which forms the subject of Palaeontology.

In order that an animal or plant may become a fossil two conditions are generally necessary: First, it must possess a skeleton of some kind or other, since the soft parts are rapidly decomposed; consequently such animals as jelly-fishes leave no trace of their existence, unless it be a mere imprint. Secondly, the organism must be covered up by some deposit, otherwise it will soon crumble to pieces. Now, since there are comparatively few places on land where material is being deposited to any great extent, it

follows that terrestrial animals will stand but little chance of being preserved; the greater number after death will remain on the surface and will in a short time be entirely decomposed. A few may become entombed in peat-bogs, in the dust and ashes thrown out by volcanoes, in the sand of sand-dunes, or by a landslip; some may be sealed up in deposits of carbonate of lime, such as the travertine thrown down by calcareous springs, or the stalagmite formed on the floor of caves; and lastly, others may be transported by running water and ultimately buried in the bed of a river, of a lake, or of the sea. Such instances, however, are of comparatively rare occurrence. In the case of aquatic animals the conditions for fossilisation are much more favourable, since deposition is more universal in water than on land. Of such aqueous deposits, those formed in the sea will enclose by far the larger number of animals on account of the greater area which these deposits cover.

The structure and composition of the hard parts vary considerably in different groups of animals and plants; some are therefore much more readily preserved as fossils than others. Thus in *Argonauta* the skeleton consists of a thin shell which is easily broken up; then again in some sponges it is formed of needles of silica, which are held together by the soft parts only and consequently easily become scattered after the death of the animal. But in other cases, as in most of the mollusks and corals, the skeleton is very strong and not easily destroyed, hence these occur abundantly in the fossil form. Perhaps even more important than the structure, is the composition of the hard parts, which, in the case of insects and some hydroids consist of a horny substance known as chitin; in diatoms, in most radiolarians, and in many sponges, of

silica; in the bones of vertebrates, chiefly of carbonate and phosphate of lime; in corals, echinoderms, mollusks and many other animals and some plants, of carbonate of lime; in most plants, of woody or corky tissue: a larger or smaller amount of organic matter is always combined with the mineral. Of these substances, chitin is with difficulty dissolved. Silica in its ordinary crystalline condition is one of the most stable of minerals, but when secreted by an animal or plant it is glassy and isotropic (*i.e.* singly refracting and without effect on polarised light), and is dissolved with comparative ease, so that such skeletons may be entirely removed by the action of percolating water. In organisms with calcareous skeletons the carbonate of lime is readily dissolved by water containing carbonic acid, but the degree of solubility varies according to the condition in which the carbonate of lime is present. In some animals it occurs as aragonite, in others as calcite. Of these two minerals, aragonite is the harder and heavier, its specific gravity being 2·93, whilst that of calcite is only 2·72; aragonite crystallises in the rhombic system, calcite in the hexagonal. Fossil calcite shells (*e.g. Pecten opercularis*) are translucent, their surface is compact, but their interior porous; on the other hand the aragonite shells (*e.g. Pectunculus glycimeris*) are opaque, and have a chalky appearance but a compact structure throughout. If a shell of each kind be suspended in water containing carbonic acid, it will be found that the one composed of aragonite will lose, in the same time, a much greater proportion of its weight than the other. Further, the calcite shell remains firm longer than the aragonite, the latter being soon reduced to the consistency of kaolin or china-clay. This difference, however, does not appear to be due directly to mineral composition, for Cornish and Kendall found that when

crystals of calcite and aragonite were powdered and placed in carbonic acid solutions of the same strength, the aragonite was *not* acted on more rapidly than the calcite, and the same result was obtained with powdered fossil shells. From all these considerations, it is not surprising to find that in some strata the aragonite skeletons have entirely disappeared, whereas those formed of calcite remain. This will obviously be most likely to occur in pervious beds through which water containing carbon dioxide percolates. A striking instance of the difference in the solubility of calcite and aragonite was furnished by some specimens of the common edible mussel, *Mytilus edulis*, in which the inner layer of the shell is formed of aragonite and the outer of calcite; Sorby found specimens in the raised beach at Hope's Nose, Torquay, which had lost the inner layer but not the outer. Similarly, in specimens of *Spondylus* from the Chalk, the inner layer of the shell has been completely removed, but the outer is left. In some cases aragonite is replaced by calcite, but then the organic structure is entirely destroyed, and we get merely a mass of calcite crystals. Calcite is never replaced by aragonite.

The mineral character of the skeleton of the chief calcareous organisms is as follows:—

Foraminifera.—The vitreous forms consist of calcite, the porcellanous probably of aragonite.

Porifera.—Calcareous sponges of calcite.

Anthozoa.—The Alcyonaria are of calcite, except *Heliopora*, which is of aragonite; the Madreporaria are of aragonite.

Echinoderma.—All of calcite.

Polyzoa.—Chiefly calcite.

Brachiopoda.—All of calcite.

Lamellibranchia.—Many consist entirely of aragonite, but *Anomia*, *Ostrea*, and *Pecten* of calcite. In *Pinna*, *Mytilus*, *Spondylus*, *Unio*, and *Trigonia*, the inner layer is of aragonite, the outer of calcite.

Gasteropoda.—The majority are formed of aragonite, but *Scalaria* and some species of *Fusus* are of calcite. In some (*e.g. Patella*, *Littorina*) the outer layer is calcite.

Cephalopoda.—*Nautilus*, *Spirula*, and *Sepia* are mainly aragonite, as also were probably the Ammonites. *Argonauta* and the guard of *Belemnites* are calcite.

Crustacea.—The shell consists of chitinous material usually containing calcite, and often some phosphate of lime.

The condition in which fossils occur depends, as we have seen, on their original composition and on the material in which they are embedded. The chief types are the following:—

1. *The entire organism preserved.* Occasionally the soft parts of the organism are preserved as well as the skeleton, the whole having suffered very little change. Instances of this are, (*a*) the woolly rhinoceros and mammoth found frozen in the mud and ice in Northern Siberia, and (*b*) insects and plants encased in fossil resin, known as amber, found in the Oligocene beds on the Baltic shores of Prussia and in the Tertiary beds near Cromer.

2. *The skeleton preserved almost unchanged.* Sometimes when the skeleton alone is preserved, it remains almost in its original condition, except that it has lost its organic matter. Thus the shells in the Pliocene beds of England differ from living ones only in being lighter, more porous and generally colourless. In some instances a certain amount of mineral matter, such as carbonate of lime, has

been added to the skeleton, making it heavier and more compact.

3. *Carbonisation.* In some plants, and in animals with chitinous skeletons, such as graptolites, the original material usually becomes carbonised. The organism undergoes decomposition and loses oxygen and nitrogen, the relative percentage of carbon therefore increasing. The changes are similar to those which occurred during the conversion of vegetable matter into coal.

4. *A mould of the skeleton.* Sometimes the skeleton disappears entirely, a mould only remaining: this is especially the case when it consists of aragonite and is embedded in a porous stratum. After the shell of a mollusk has become covered up with sediment, and the soft parts have been decomposed, the interior becomes filled with the same material. Water containing carbonic acid subsequently percolates through the rock and carries away the shell as bicarbonate of lime, so that there is left only a mould of the interior and of the exterior, the space between the two being that which was originally occupied by the shell and, if filled with wax, will give an exact model of it. Excellent examples of this mode of fossilisation are seen in some mollusks from the Portland Oolite, *e.g. Cerithium* and *Trigonia.* Sometimes after the shell has been removed the space left becomes filled up with mineral matter carried in by percolating water; this has the form of the original skeleton but obviously not its internal structure.

The interior of the shells of foraminifera may, soon after the death of the animal, become filled with glauconite (silicate of iron and alumina); subsequently the shell itself often disappears, leaving only the internal cast. Glauconite occurs in this way in the various greensand strata, and

also in some of the deep-sea deposits at the present day. Somewhat similarly the shells of sea-urchins occurring in the Chalk are sometimes filled with flint; in such cases the shell when buried did not become filled with Chalk, but remained empty until flint was deposited in it from percolating water containing silica in solution.

5. *Petrifaction.* In some deposits the fossils show the minute structure as well as the form of the organism, but the original material of the skeleton has been replaced by another mineral. Thus we find fossil wood which shows the cells and vessels just as in existing trees, but in which the walls are formed of silica instead of cellulose. The change has gone on in such a manner that as each particle disappeared its place was taken by a particle of silica. The chief minerals which replace the original substance of organisms in this manner are:—

(i) Carbonate of lime; calcite sometimes replaces the silica of sponges.

(ii) Silica, as in the fossils from the Blackdown Greensand, and the Thanet Sands near Faversham; also in the wood of the Purbeck dirt-bed in the Isle of Portland.

(iii) Iron pyrites; *e.g.* Ammonites from the Oxford Clay, Lias, etc., and some graptolites.

(iv) Oxide of iron, in the form of limonite in some fossils from the Dogger (Inferior Oolite) of Yorkshire and the Lower Greensand of Potton, etc., and as hæmatite in fossils from the Carboniferous Limestone of Cumberland.

(v) In rare cases there are other replacing minerals, such as sulphate of lime, barytes, blende, galena, malachite, vivianite, and spathic iron.

6. *Imprints* The footprints of animals and the impressions of jelly-fishes are sometimes found in the rocks, and these, although forming no part of the animal itself, are nevertheless regarded as fossils.

In endeavouring to discover the changes which have taken place on the earth in past geological times, the evidence furnished by fossils is of primary importance. Each great group of the stratified rocks, known as a system, is characterised by a particular assemblage of genera and species, some of which are confined to it and enable us to identify the system. In a similar manner, the smaller divisions—the series and stages—are each characterised by the presence of certain fossils, which do not occur above or below. Further, it is found that the fauna of the smallest division (stage or group of beds) is not of uniform character throughout; although there may be no change in the nature of the rock, some of the species and varieties which are abundant at one level will become rare or will disappear entirely in passing to higher or lower horizons. Consequently, a set of beds may be divided into belts or zones, the general aspect of the fauna of each zone being somewhat different from that of the others, but between these divisions there will be no break either physical or palæontological. If then we have determined the order of succession of the formations in any one area by means of their relative positions, the newer resting on the older, it is fairly easy in any other district, merely by examining the fossils, to refer any set of beds to its proper position in the geological record. But although this law of the identification of strata by the fossils which they contain is of great value, it must not be applied without some caution, for even if two formations were deposited at exactly the same time, it does

not necessarily follow that all the genera and species found in the two will be identical. Thus for instance in the seas at the present day the same forms of life do not occur in all parts; animals which live in water of moderate depth are distributed in provinces which depend largely on climatic conditions, each province possessing some forms peculiar to itself. The organisms now being entombed in deposits formed, say, off the British coasts, will as a whole be different from those off the Canary Islands; but still, some of the species and many of the genera will be common to both areas, and would enable us to identify the two deposits as having been formed within the same general period, though perhaps not to prove them absolutely synchronous. Then again there is a distribution of organisms according to the depth of the sea, and the nature of the sea-bottom; so that the fauna of a deep-water formation will necessarily be different from that of a shallow-water one, and that of a sandy deposit different from that of a mud. But in addition to the animals living on the sea-bottom there are others which live near the surface of the ocean, far from land; such *pelagic* forms have a wider geographical range than those which live on the sea-floor in shallow water, and are consequently of great value in determining, as of the same age, deposits found in widely-separated localities.

In addition to their chronological value, fossils are also important in indicating the conditions under which the formations were deposited. In the case of the later beds, where most of the fossils belong to genera which are still existing, it is easy to distinguish a marine deposit from one formed in freshwater or on land. Even in the rocks of earlier periods, in which most of the genera are extinct, we may recognise a marine deposit by the presence of such

animals as radiolarians, corals, echinoderms, brachiopods, pteropods, cephalopods, or cirripeds, which at the present day are found only in the sea.

The depth of the sea in which a formation was deposited can be estimated when the fossils belong to living species; when the species are extinct some idea may be formed if the genera to which they belong are found chiefly at some particular depth at the present day. In attempting such determinations it must be remembered that the sea-bottom down to a depth of nearly 50 fathoms may be disturbed by the action of waves and currents in the sea; consequently the animals living on the bottom in shallow water are liable to be carried from their original home to higher or lower levels. One of the surest indications that a formation was laid down in shallow water and not far from land is furnished by the association of the fossil remains of land animals and plants with marine species; another, by the presence of mollusks such as *Pholas*, *Saxicava* and *Lithodomus*, which bore into rocks, and at the present day are found only in shallow water. The proximity of a shore-line is also indicated when the assemblage of fossil forms resembles in general character the faunas which live in littoral regions at the present day. When evidence of the existence of a shore-line is found it is obviously possible to gain some idea of the distribution of land and sea in past times.

The nature of the climates of past ages may be judged to some extent by the character of the fossils; the evidence furnished by land-plants is particularly valuable, since their distribution is determined largely by temperature and is better marked than in the case of marine animals. As far as the latter are concerned it is only when we are dealing with modern species that we can, as a rule, speak

with any degree of certainty on this subject; this is owing to the fact that at the present day the individual species of the same genus have often a very different distribution, some being found in warm, others in cold, regions. Even when all the fossils in a formation belong to extinct species, the assemblage of genera is sometimes such as marks some region at the present day; thus, for example, in the London Clay we find that many of the genera of mollusks are now characteristic of tropical or sub-tropical seas.

The study of fossil animals and plants is of the highest importance to the biologist, not only because they include the ancestors of modern species, but because among fossil forms we find many groups (*e.g.* Graptolites, Cystids, Blastoids, Trilobites, Eurypterids), which are altogether extinct, and which often throw light on the relationship of existing animals and plants. Others (*e.g.* Crinoids, Brachiopods, Nautiloids) are represented at the present day by few forms only, but were, in past ages, very abundant; consequently no adequate knowledge of such groups of animals can be obtained from the study of living examples only. In some cases the ancient forms serve to connect groups which, at the present day, appear to be quite distinct; thus, for example, the earliest known bird (*Archæopteryx*, from the Solenhofen Limestone, Upper Jurassic) shows, in several important characters, affinities to the Reptiles.

From the point of view of the biologist, the greatest interest in Palæontology is found in the bearing it has on the subject of evolution: it is only by a study of the stratigraphical succession of fossil forms that the race-history or phylogeny of animals and plants can be traced with certainty; but in attempting such investigations a great difficulty is presented by the imperfection of the record of

fection of the geological record:—

the life of past ages, since only a very small proportion of the animals and plants has been preserved, and often in an imperfect manner. We have already seen several reasons why this record must be imperfect; some animals are without hard parts, while others, particularly land animals, frequently do not become covered up with sediment. Further, the remains of animals which were originally present in the rocks have been, in some cases, dissolved by percolating water, or to a great extent obliterated by the metamorphism which the rock has undergone. Then again the record of life is incomplete because of the breaks in the succession of the stratified rocks; these breaks have been caused sometimes by denudation having removed a great thickness of rocks, in other cases by a temporary absence of deposition. Even when there is no break in the succession due to these causes a further difficulty in tracing out phylogeny may be introduced by changes taking place in the physical conditions during the deposition of a series of beds; thus there may have been alterations in the depth of the sea, in the nature of the sediment on the floor, or in the temperature of the water; in each case the physical change would re-act on the fauna tending to cause the animals living on the sea-floor to migrate to other regions where conditions favourable to their mode of life could be found. When such migrations occurred the descendants of the animals which lived when one stratum was deposited would not be found fossil in the overlying beds of the same area.

Notwithstanding this imperfection of the record and the effects of changing physical conditions, many groups of animals are found to undergo gradual modification when traced through series of strata or formations. For example, in the Pliocene deposits of Slavonia there are numerous

shells of pond-snails (*Viviparus* or *Paludina*); and specimens found at the top and bottom of the formation, and also at certain intervening levels, differ so much from one another that they appear to belong to distinct species. When, however, examples are collected from all the beds of the formation, the apparently distinct species are seen to be connected by intermediate forms, and a series, showing a gradual passage from the species found in the lowest bed to that in the highest, can be obtained. Similarly in the English Chalk, during the deposition of which the physical conditions continued more nearly uniform than in most other formations, it is found that the sea-urchins, starfishes, etc. undergo slow and gradual changes in various characters when traced from lower to higher horizons.

In several groups of Tertiary Mammalia there is also evidence of gradual modification in structure; thus the earliest known forerunner of the horse, found in the Eocene beds, possessed five toes, and was succeeded in later times by forms with successively fewer toes, until in the Pliocene, the existing type of horse, with only one toe and splint-bones, appeared; other gradual changes also occurred in the character of the teeth, etc.

In attempting to work out phylogeny, in addition to the stratigraphical method just described, the method of comparative anatomy and often the method of ontogeny (or development of the individual) can be used in the case of fossils. In the course of the development and growth of an animal, various stages, which often present resemblances to the adults of other animals, are passed through. The 'recapitulation theory' supposes that the changes seen during the development of the individual (ontogeny) are, in a general way, a rapid but often incomplete repetition of those which occurred in its race-history (phylogeny).

Palæontology has, in many cases, given support to this view, by showing that successive stages, similar to those passed through in the development of an animal, also occurred in the history of its race, as seen in the geological record.

On the whole the evidence of Palæontology favours the view that evolution proceeded by slow and gradual modifications; but there were also times, especially in the early history of various groups, when evolutionary changes went on more rapidly. There is also evidence indicating that evolution was *orthogenetic*—that the evolutionary changes in any one group of animals proceeded in definite directions for considerable periods of time; and further, that allied groups, descended from the same ancestral stock, have passed through similar or parallel stages in their evolution quite independently of one another and of external conditions, suggesting that the lines of evolution in the various groups were determined by something inherited from the common ancestor. Examples of this are seen in the Chalk starfishes, in the mode of branching of graptolites (p. 69), in the development of horns in different evolutionary series of Titanotheres, and in the evolutionary history of various other groups of Tertiary mammals.

In a natural classification of animals an attempt is made to place together in the same group those forms which are connected by descent; such a classification, if perfect, would be of the nature of a genealogical tree. Each main division is termed a Phylum and includes animals built on the same fundamental plan and believed to have descended from one ancestral stock. Each Phylum is divided and subdivided into smaller and smaller groups, known as Classes, Orders, Families, Genera, and Species.

A species includes a group of individuals very closely related to one another, which have descended from the same ancestors and can give rise to offspring which are fertile among themselves; such individuals usually differ from one another to only about the same degree that offspring of the same parents may differ. One species is generally distinguished from another by such characters as ornamentation, shape, relative proportion of parts, and size. In some species one or more groups termed *varieties* may be recognised, and are distinguished from the other forms included in the species by some slight, but fairly well-marked and constant modification. Varieties are frequently connected with the special physical or biological conditions under which they are living. The varieties in some species pass into one another by intermediate forms; but others appear to be fairly distinct and may be regarded as incipient species.

Sometimes two groups of individuals resemble each other so closely that they might be regarded as belonging to the same genus or even to the same species, but they have descended from different ancestors since they are found to differ in development (ontogeny) or in their palæontological history; this phenomenon, of forms belonging to different stocks approaching one another in character, is known as *convergence* or *heterogenetic homœomorphy*, and may occur either at the same geological period or at widely separated intervals. Thus the form of oyster known as *Gryphæa* has originated independently from oysters of the ordinary type in the Lias, in the Oolites, and again in the Chalk; these forms found at different horizons closely resemble one another and have usually been regarded as belonging to one genus (*Gryphæa*), but they have no direct genetic connection with one another.

Similarly in various species of Terebratulids a double fold or biplication has arisen in the front part of the shell, thus giving considerable resemblance to different species which are not closely related to one another. Then again sutures similar to those of *Ceratites* from the Trias are developed in some Chalk Ammonites which have no genetic connection with *Ceratites*.

Also, animals belonging to quite distinct groups may, when living under similar conditions, come to resemble one another owing to the development of adaptive modifications, though they do not really approach one another in essential characters; thus analogous or parallel modifications may occur in independent groups—such are the resemblances between flying reptiles (Ornithosaurs) and birds, and between sharks, ichthyosaurs and dolphins.

PHYLUM PROTOZOA

Classes.	*Orders.*
1. Gymnomyxa (Sarcodina)	1. Foraminifera. 2. Radiolaria. 3. Others not found fossil.

2. Flagellata or Mastigophora (not fossil).
3. Infusoria (not fossil).
4. Sporozoa (not fossil).

THE Protozoa include the lowest forms of animals, such as *Amœba*, *Vorticella*, and *Globigerina*. The body is usually very small, and consists in many cases of one cell only, in others of more than one, but the cells never form tissues as they do in all other animals. A cell consists of *protoplasm*—a viscid or semi-fluid living substance containing granules; in the centre of the cell is a denser, usually spherical body called the *nucleus*—sometimes more than one is present.

In some Protozoa (the *Gymnomyxa*) the protoplasm is naked, and consists of an inner granular mass and a thin, clear, outer layer; such forms are further characterised by having no definite shape, by being able to take in food at any part of the body, and by possessing the power of throwing out lobes or filaments of protoplasm known as *pseudopodia*. In others (the *Flagellata* and *Infusoria*) the protoplasm is surrounded by a firm membrane or cuticle which gives the animal a definite form; the food is generally taken in at one permanent aperture, and pseudopodia are seldom present, but the surface is provided with *cilia* or

flagella, which are fine threads of protoplasm having a definite form and a rhythmic movement.

Reproduction in the Protozoa takes place usually by fission (*i.e.* division into two parts) and sometimes by the formation of spores. In some cases conjugation of two or more individuals occurs, representing to some extent sexual reproduction. In some of the Protozoa there is no skeleton, but in others a shell is formed.

The Protozoa can be divided into four main groups, (1) the Gymnomyxa, (2) the Flagellata, (3) the Infusoria, (4) the Sporozoa; no examples of the last three divisions have been definitely recognised in the fossil state.

CLASS I. GYMNOMYXA (SARCODINA)

The members of this group possess no external membrane (cuticle), and are able to throw out pseudopodia, by means of which movement takes place and food is obtained.

The Gymnomyxa or Sarcodina are divided into several orders, of which only two have been found fossil, namely, the Foraminifera and the Radiolaria.

ORDER I. FORAMINIFERA

The Foraminifera are characterised by their thread-like pseudopodia, which frequently branch and anastomose; and by possessing in most cases a shell or test, which may be calcareous, arenaceous, chitinous, or gelatinous.

The calcareous forms are by far the commonest, and in these, two kinds of shell may be distinguished, namely, the *vitreous* and the *porcellanous*. In the vitreous, the shell has a glassy appearance, and is perforated by innumerable tubes for the passage of the pseudopodia; in some forms (*e.g.* *Rotalia*) these tubes are $\frac{1}{3000}$ of an inch in diameter, but in others (*e.g.* *Operculina*) only $\frac{1}{16000}$ of an inch. In

the porcellanous forms the shell, when viewed by reflected light, is opaque and white, having the appearance of porcelain; it is not perforated by tubes, but possesses one or two large apertures through which most of the pseudopodia pass out—some, however, are given off from the layer of protoplasm which covers the surface of the shell. In these porcellanous Foraminifera the shell is sometimes pitted, producing at first sight the appearance of perforation.

In the arenaceous forms the shell consists of foreign particles joined together by a cement. The particles are usually grains of sand (commonly quartz), but sometimes sponge spicules, or the shells of other Foraminifera. The cement may be formed of chitinous, calcareous, or ferruginous material. The shell is often imperforate.

The chitinous forms (*e.g. Gromia*) do not occur as fossils.

The shell of the Foraminifera varies considerably in form and structure; in some genera it consists of a single chamber, when it is said to be *unilocular*, as in *Lagena* (fig. 3 F) which is generally flask-shaped. In other cases it consists of several chambers communicating with one another, either by perforations in the walls (septa) between them, or by larger openings. In these *multilocular* forms the shell grows by the addition of a new chamber at the end of the one last formed; this takes place by the protrusion, through the aperture or mouth of the shell, of a mass of protoplasm, at the surface of which the wall of a new chamber is formed either by the secretion of material or by cementing of foreign particles. The arrangement of the chambers in the multilocular Foraminifera is very varied; they may be placed in a straight line as in *Nodosaria* (fig. 4 H), in a curved line as in *Dentalina*, in a plane-spiral as in *Cristellaria* (fig. 3 G), or in a helicoid

spiral as in *Rotalia* (fig. 3 L, M). The earlier whorls in some spiral forms are partly or entirely covered by the later ones, so that sometimes the last whorl only is visible on the exterior (*e.g.* *Cristellaria*); but when the later chambers are merely attached to the extremities of the earlier ones, all the whorls can be seen (*e.g.* *Operculina*). Some genera, such as *Textularia* (fig. 3 E), have two rows of chambers placed side by side; others (*Tritaxia*) have three. In some cases (*e.g.* *Orbitolites*) there are numerous chambers arranged in concentric rings instead of in a spiral.

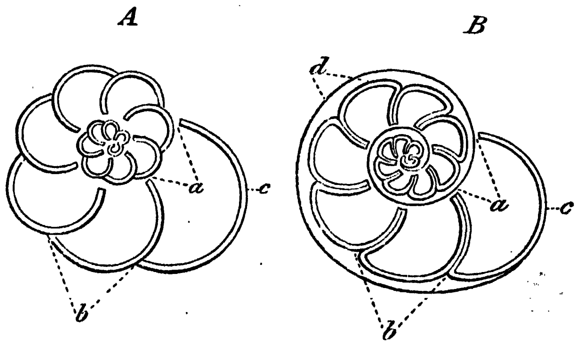


Fig. 1. A, section of a foraminifer in which each septum is formed of a single lamella. B, in which the septum is formed of two lamellæ. *a*, passages between the chambers; *b*, septum; *c*, anterior wall of last chamber; *d*, supplemental skeleton. (After Carpenter.)

In the porcellanous and the simpler vitreous Foraminifera each septum (fig. 1 A, *b*) consists of a single lamella which is really the front wall of the preceding chamber; but in the higher vitreous forms each septum (fig. 1 B, *b*) is formed of two lamellæ, owing to the fact that when a new chamber is added to the shell a new wall is secreted next to the front wall of the last chamber. The shell of the vitreous Foraminifera is at first thin, but may afterwards increase in thickness by the addition of material at

the surface; in the higher vitreous forms the outer layers constitute what is known as the *supplemental skeleton* (fig. 1 B, *d*), which is traversed by numerous canals connected with canals in the septa and other parts.

A considerable number of the Foraminifera, especially the higher forms, are *dimorphic*—that is to say, there are two forms of the same species. This fact was first noticed in specimens of *Nummulites* from the Eocene deposits. In one form, the first or initial chamber, which is seen at the centre when the shell is split, is large and more or less

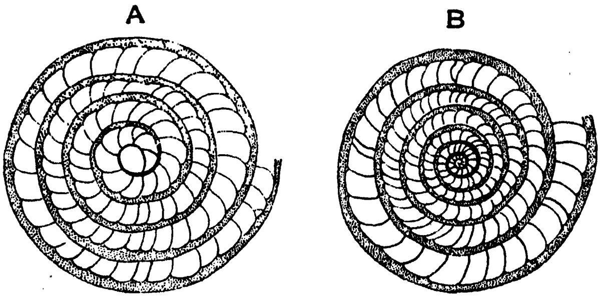


Fig. 2. Dimorphism of *Nummulites lævigatus*, Bracklesham Beds (Eocene), Selsea. A, section of the entire shell of the megalospheric form × 9. B, section of the *central* part of the microspheric form × 9.

spherical and is called the *megalosphere* (fig. 2 A); in the other it is much smaller and is known as the *microsphere* (fig. 2 B). These two forms are found associated together, and were, at one time, described as different species. In the microspheric type the shell commonly, but not always, grows to a larger size than in the megalospheric type, and individuals of the former are much less numerous than of the latter; in other respects the two are similar. The relationship of the microspheric and megalospheric shells has been elucidated by a study of the life-history of *Poly-*

stomella and other living Foraminifera. When reproduction takes place in the microspheric form all the protoplasm passes out of the shell and divides into spherical masses, each of which secretes a shell and develops into a megalospheric individual. In the reproduction of the megalospheric form the protoplasm divides into small rounded portions which pass out of the shell as moving spores—zoospores; it is believed that two zoospores from different individuals conjugate and give rise to a microspheric individual. There are, therefore, two modes of reproduction—one asexual, the other apparently sexual, which alternate.

For convenience of reference the Foraminifera may be divided into three groups, the characters of which are based on the structure and composition of the shell; but this cannot be regarded as a natural classification since it sometimes separates allied forms, and also in some types which are usually calcareous we occasionally meet with species in which the shell consists largely of sandy material.

I. *Porcellanous Forms.*

Shell calcareous, porcellanous, not perforated by canals, but provided with one or two large apertures through which the pseudopodia pass out.

* **Miliola** (fig. 3 A—D). Shell multilocular, the early chambers spiral, the later chambers coiled on an elongated axis, each chamber forming half a convolution. In some cases all the chambers are visible externally on both sides of the shell (fig. 3 D); in others, owing to the lateral prolongations of the chambers, only the last one or two are seen (fig. 3 A—C); or it may be that more chambers are shown on one side than on the other. The external features of the shell consequently vary considerably, and on account of this and other features in the mode of coiling, the forms included under the term *Miliola* are now regarded as constituting a number of distinct genera to which the following names have been given:—*Biloculina*,

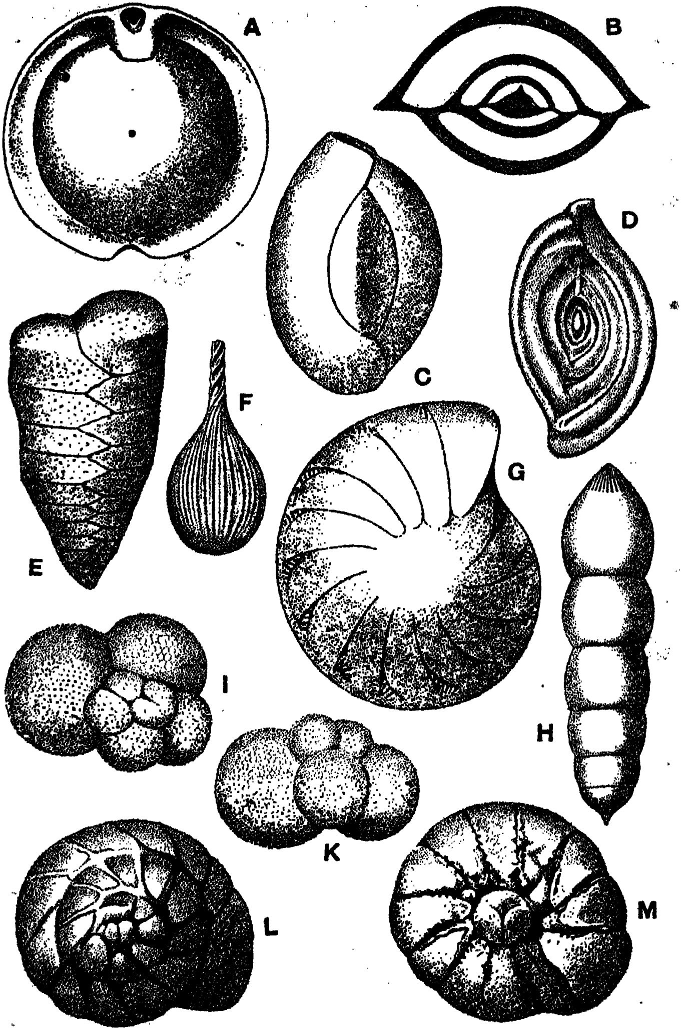


Fig. 3. Foraminifera (recent). A, B, *Biloculina depressa*. B, section. C, *Miliolina seminulum*. D, *Spiroloculina limbata*. E, *Textularia barretti*. F, *Lagena sulcata*. G, *Cristellaria rotulata*. H, *Nodosaria radicula*. I, K, *Globigerina bulloides*. L, M, *Rotalia beccari*. (After Brady.) All enlarged.

Fabularia, *Spiroloculina*, *Miliolina*, *Quinqueloculina*, etc. Trias to present day. Ex. *Miliolina seminulum*, Eocene to present day; *Biloculina ringens*, Eocene to present day; *Spiroloculina planulata*, London Clay to present day.

* **Orbitolites.** Shell discoidal, generally rather large, composed of either a small spiral part at the centre, or of one or more large central chambers, around which are many concentric rings divided into numerous chambers by radially arranged septa; the chambers of adjacent rings communicate by radial openings, and at the external margin of the last ring are pores opening to the exterior. Above and below this layer of chambers there may be other layers of smaller chambers arranged concentrically. Lias to present day. Ex. *O. complanata*, Eocene.

* **Alveolina.** Shell fusiform or elliptical, sometimes nearly globular, composed of many whorls coiled around the long axis of the shell; each whorl completely covers the one preceding it, and is divided into long chambers by partitions parallel with the axis of the shell; these are divided into smaller chambers by partitions at right angles to the others. Chalk to present day; chiefly Eocene. Ex. *A. bosci*, Eocene.

II. *Arenaceous Forms.*

Shell composed of grains of sand or other particles cemented together by chitinous, calcareous, or ferruginous material.

Saccammina. Shell usually free, compact, formed of a single spherical, pyriform, or fusiform chamber with a projecting aperture at one or both ends, or of a number of chambers united end to end. Surface smooth or nearly smooth. Ordovician, Devonian, Carboniferous, and living. Ex. *S. fusuliniformis* (= *carteri*), Carboniferous Limestone.

Lituola. Shell free, composed of coarse grains, spiral or crosier-shaped. Septa labyrinthine. Aperture simple or sieve-like. Carboniferous to present day. Ex. *L. nautiloidea*, Chalk.

* **Orbitolina.** Shell partly sandy; conical or flattened, with convex upper, and usually concave lower surface; consisting of

central compressed chambers surrounded by concentric rings of chambers. Cretaceous. Ex. *O. concava*, Upper Greensand.

Endothyra. Shell free, largely calcareous; spiral, nautiloid, or rotaliform; chambers numerous, composed of an outer calcareous, perforated layer, and an inner compact layer formed of small grains cemented together. Apertures at the inner margin of the last chamber. Carboniferous to Trias. Ex. *E. bowmani*, Carboniferous Limestone.

* **Textularia** (fig. 3 E). Shell arenaceous (in the small forms it is vitreous); conical, pyriform, or cuneiform; composed of numerous chambers in two alternating parallel series. Aperture slit-like on the inner edge of the last chamber. Carboniferous to present day. Ex. *T. globulosa*, Chalk.

III. *Vitreous Forms.*

Shell of calcite, vitreous, perforated by numerous minute canals for the passage of the pseudopodia.

Lagena (fig. 3 F). Shell unilocular, very finely perforated. Form globose, ovate, or flask-shaped. A single terminal aperture, sometimes at the end of a long neck; rarely two apertures. Surface smooth, ribbed, striated, or spinous. Upper Cambrian to present day. Ex. *L. striata*, London Clay to present day; *L. sulcata*, Silurian to present day.

* **Nodosaria** (fig. 3 H). Shell composed of a number of chambers which are circular in transverse section, arranged in a straight line, and separated by constrictions. Aperture at the apex of the last chamber. Surface smooth or ornamented with granules, spines, or ribs. Cambrian to present day. Ex. *N. zippei*, Gault and Chalk.

Cristellaria (fig. 3 G). Shell compressed, lenticular or elongate, multilocular, coiled in part or entirely in a plane spiral; each coil usually covers the one preceding it. Upper Cambrian to present day. Ex. *C. rotulata*, Chalk.

Globigerina (fig. 3 I, K). Shell perforated by large canals; chambers globular, few, arranged in a plane or helicoid spiral, each chamber opening by a large aperture into the central cavity of the

spire. No supplemental skeleton. Pelagic forms usually with spines. Trias to present day. Ex. *G. cretacea*, Chalk.

Orbulina. A single spherical chamber, with perforations of two sizes. Sometimes with smaller chambers (similar to a *Globigerina*) inside the large spherical one. Lias to present day. Ex. *O. universa*, Lias to present day.

Rotalia (fig. 3 L, M). Test very finely perforated, multilocular. The chambers arranged in a helicoid spiral, so that on the upper surface all the whorls are seen, on the lower only the last one. The aperture is in the form of a curved slit on the lower surface of the last chamber. The septa are usually formed of two layers with canals between the layers. A supplemental skeleton is often present. Lower, Cretaceous to present day. Ex. *R. beccari*, Miocene to present day.

Calcarina. Test lenticular, spiral, with only the last whorl visible on the base. Supplemental skeleton greatly developed, traversed by numerous canals, and projecting as long spines from the margin. Chalk to present day. Ex. *C. calcitrapoides*, Chalk.

* **Fusulina.** Shell fusiform, composed of elongated whorls; each whorl completely covers the preceding one, and is divided by septa into a number of chambers, which may be again divided into smaller chambers. Adjoining chambers communicate by a slit at the middle of the base of each septum. Septa folded, each consisting of a single layer. Aperture in the form of a fissure. Carboniferous and Permian. Ex. *F. cylindrica*, Carboniferous Limestone.

Amphistegina. Shell lenticular, with sharp edge; the upper and lower surfaces unequally convex; formed of numerous chambers coiled in a plane spiral, each coil almost completely enclosing the preceding one. Septa formed of a single layer. Supplemental skeleton at the centre of the shell. Aperture similar to that of *Rotalia*. Carboniferous, and Miocene to present day. Ex. *A. haueri*, Miocene.

* **Nummulites** (figs. 2, 4). Shell lenticular in form, and composed of a large number of whorls coiled in a plane spiral. Usually each whorl completely covers the preceding one by means of the lateral prolongations of the chambers, so that externally only the last whorl of the shell is visible. The whorls are divided into

chambers (*c*) by septa (*b*) which are slightly curved backwards; each chamber communicates with the neighbouring one by means of a median fissure at the inner margin of the septum. Each septum is formed by two lamellæ. A supplemental skeleton is present, part of it forming what has been termed the 'marginal cord' (*a*). The general shell-substance is minutely perforated, and a system of canals also traverses the septa and supplemental skeleton. Aperture in the form of a slit at the inner margin of the last chamber. The shell splits readily into two similar parts along the median plane, owing to the relatively large size of the parts of the chambers occurring there. The earliest species of *Nummulites* occurs in the

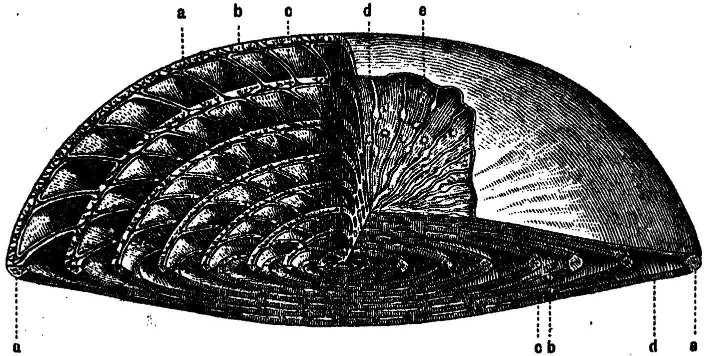


Fig. 4. *Nummulites*, showing vertical and horizontal sections. *a*, marginal cord with canals (supplemental skeleton); *b*, septum, with canals; *c*, chambers; *d*, test; *e*, pillars of the supplemental skeleton. (After Zittel.) Enlarged.

Carboniferous Limestone of Belgium; others have been recorded from the Upper Jurassic of Amberg (Bavaria); the genus attains its maximum in the Eocene; only one or two rather rare forms are living, one of which (*N. cummingi*) is found in shallow water in tropical and sub-tropical regions. In the English Eocene the genus is found in the Barton and the Bracklesham Beds. Ex. *N. lævigatus*, Bracklesham Beds.

Operculina. Similar to *Nummulites*, but whorls fewer and rapidly enlarging, all visible externally; each of the earlier whorls partly encloses the preceding one. Cretaceous to present day. Ex. *O. complanata*, Miocene.

Orbitoides. Test lenticular or discoidal, composed of a median layer of rectangular chambers arranged in concentric rings which are often incomplete; the chambers of adjacent rings communicate by oblique passages. Above and below this layer are numerous layers of smaller chambers; these chambers are flattened and irregular in form, placed one above the other in piles, and arranged more or less concentrically. The test is minutely perforated, and canals traverse the septa and marginal cord as in *Nummulites*; the septa are also formed of two lamellæ. Chalk to Miocene; chiefly Eocene. Ex. *O. papyracea*, Eocene.

Distribution of the Foraminifera.

The majority of the Foraminifera are marine, most of them living on the sea-bottom. A few however, as for instance *Globigerina*, exist at or near the surface in the open ocean, and these are very important on account of their abundance, especially in warm seas. The distribution of the pelagic Foraminifera in the open ocean, as well as those which live on the sea-floor in shallow water, is influenced largely by temperature; the former are more numerous in warm regions and in warm ocean-currents than in colder water, whilst the species of the latter often have their range determined by temperature and depth.

The Foraminifera found in the Palæozoic deposits are mainly vitreous and arenaceous forms. They appear first in the Cambrian rocks, but are comparatively rare until the Carboniferous, in which some beds are formed largely of their shells, as for instance, the *Saccammina*-limestone of the north of England and Scotland, the *Endothyra*-limestone of North America, and the *Fusulina*-limestone of Russia, China, Japan and North America. The Foraminifera are mostly of small size in the Permian of England; they are comparatively rare in the Trias, but become abundant in the Jurassic, where, however, rock-building

types are generally absent. In the Lias the introduction of numerous vitreous species (*Nodosaria, Cristellaria*, etc.), many of which appear to be allied to forms now living in tropical or warm-temperate regions only, is noteworthy; some porcellanous forms belonging to the *Miliola* group are also fairly common. A larger number of genera and species are found in the Middle and Upper Jurassic than in the Lias.

The Order continues to be well represented in the Cretaceous formations, particularly in the Gault and Chalk—*Orbitolina, Calcarina, Globigerina, Rotalia*, etc. being common. Some beds of the Chalk, especially the *Micraster* zones and the Chalk Rock, are largely composed of Foraminifera such as *Globigerina, Textularia, Bolivina, Flabellina.*

The Foraminifera attain their greatest development in Tertiary and recent times. In the Eocene deposits *Nummulites* is often extremely abundant and of large size, forming the greater part of the massive Nummulitic Limestone of Southern Europe, Egypt, Asia Minor, and the Himalayas; *Miliola, Orbitolites, Alveolina, Operculina,* and *Orbitoides* are also important rock-building-forms in the Eocene period. In the English Eocene, Foraminifera are numerous in the Thanet Sands and the London Clay; in the Barton and Bracklesham Beds *Nummulites, Miliolina, Alveolina*, etc. occur. *Amphistegina* is abundant in the Miocene. A large number of forms occur in the Pliocene deposits of East Anglia and of St Erth in Cornwall.

The genera and species of the Foraminifera have generally, as might be expected from their low organisation, a long range in time; some of the species which occur in the Palæozoic are still living.

ORDER II. RADIOLARIA

In the Radiolaria the body consists of a central mass of protoplasm, enclosed in a membrane known as the *central capsule* (fig. 5, 2). The intracapsular protoplasm contains one or more nuclei, and is continuous, through pores in the capsule, with a layer of protoplasm outside the capsule; this layer gives off thread-like pseudopodia, which occasionally unite. A skeleton (fig. 5, 1) is generally present and is usually composed of silica; but in one

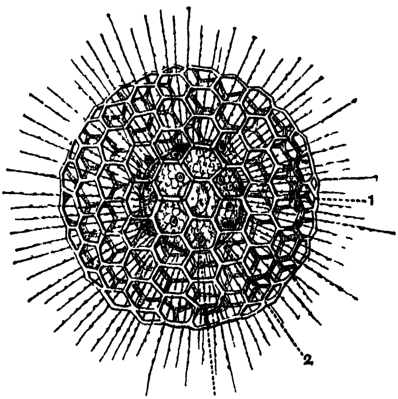
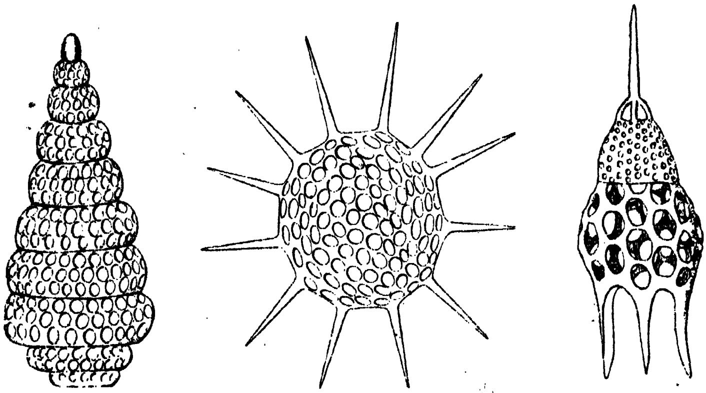


Fig. 5. *Heliosphæra inermis*. ×350. Recent. (After Bütschli.) 1, skeleton; 2, central capsule; 3, nucleus. Pseudopodia project from the surface.

group of Radiolaria it consists of a substance which was formerly regarded as horny in nature and termed acanthin, but is now believed to consist of strontium sulphate. The skeleton shows great diversity of form and complexity (fig. 6); it may be entirely outside the central capsule or partly within, and consists either of isolated spicules, or of a lattice-like or reticulate structure of varying shape, frequently with projecting spines.

The Radiolaria are all marine and mainly pelagic; the majority live between the surface and a depth of 200 fathoms, but a few forms occur in much deeper water. They have a very wide geographical distribution, being found in all climates, but show the greatest variety of forms in the seas between the tropics; they are also abundant in individuals in the Arctic seas, but the variety of forms is relatively small. In some of the deeper parts of the Pacific and Indian Oceans the empty shells of these



A B C

Fig. 6. Fossil Radiolaria. A, *Lithocampe tschernyschewi*, Devonian. B, *Trochodiscus longispinus*, Carboniferous. C, *Podocyrtis schomburgki*, Barbados Earth (Tertiary). All largely magnified.

animals settle and accumulate on the sea-bottom, forming a siliceous deposit known as 'Radiolarian ooze.' Only those Radiolaria in which the shell consists of silica are preserved as fossils.

Cayeux has described as Radiolaria some bodies found in the Pre-Cambrian rocks of Brittany; they are much smaller than later forms of the group, and are thought by some authors to be simply inorganic aggregations. Im-

perfectly preserved Radiolaria have been recorded from the Cambrian of Thuringia.

In Britain the earliest examples of the Radiolaria occur in the Ordovician rocks of the south of Scotland, where they form beds of chert; others which are perhaps of nearly the same age, have been found in a chert from Mullion Island (off the west coast of the Lizard). A few specimens have been noticed in the Carboniferous Limestone of Flintshire; whilst in the Carboniferous Limestone of South Wales and in the Lower Culm of Devon and Cornwall these organisms contribute largely to the formation of thick beds of siliceous rock (cherts, etc.)—some, at any rate, of these deposits appear to have been formed in shallow water. At several localities on the continent Radiolaria are fairly common in the Mesozoic formations, but in England only a few have been recorded from the Lias, the Lower Greensand, the Upper Greensand, the Cambridge Greensand, and the Chalk. In the Tertiary some have been obtained from the London Clay of Sheppey. A very important Radiolarian formation of late Tertiary age covers large areas in the Island of Barbados, and is known as the 'Barbados Earth'; it resembles very closely the modern Radiolarian ooze mentioned above, and is probably a deep-sea deposit.

PHYLUM PORIFERA

Classes.	*Orders.*
1. **Hexactinellida.**	
2. **Demospongiæ**..............	1. **Myxospongida.**
	2. **Ceratosa.**
	3. **Monaxonida.**
	4. **Tetraxonida.**
	5. **Lithistida.**
	6. **Octactinellida.**
	7. **Heteractinellida.**
3. **Calcarea.**	

SPONGES vary greatly in form, size, and complexity of structure. A simple type is similar to a vase or hollow sac, fixed by the lower end, and with an opening or *osculum* at the upper extremity. The wall of such a sponge is thin, and perforated by a large number of pores through which water flows into the central or *gastral cavity* and passes out by the osculum; by this means the sponge is provided with food and oxygen and gets rid of waste matters. The wall of the sponge consists of two layers—an outer or *dermal* and an inner or *gastral*; the dermal (fig. 7, 2) is formed of a surface-layer of flattened cells, with a gelatinous layer beneath containing various cells, some of which secrete the elements of the skeleton. The gastral layer (fig. 7, 3) consists of a single layer of cells, each cell being provided with a collar-like projection, in the centre of which is a long flagellum; the circulation of water through the sponge is produced by the movements of these flagella.

A simple form like that just described is found in the young stages of many sponges which afterwards, in their

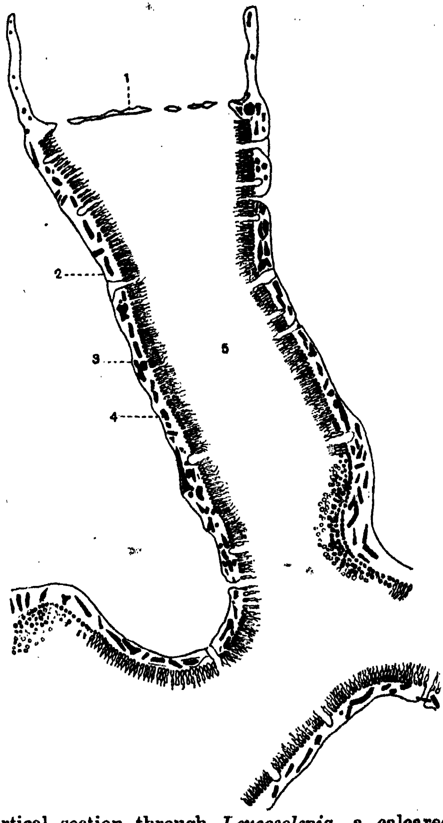


Fig. 7. Vertical section through *Leucosolenia*, a calcareous sponge. Highly magnified. (From Minchin.) 1, sieve-like membrane covering the osculum; 2, outer layer; 3, collar or flagellated cells (the pointer should have been continued to indicate the cells lining 5); 4, spicules; 5, gastral cavity.

adult condition, are much more complex. Owing to the growth of the sponge-wall being unequal in different parts,

either folds or tube-like projections are formed, and these subsequently become more or less completely fused, so that the wall is much thickened (fig. 8) and is traversed by canals which are really spaces enclosed between the folds and outgrowths. In such forms the flagellated cells are frequently confined to chambers in the sponge-wall (fig. 8, 4). Canals, called *incurrent* or *inhalent* canals (2), pass from the surface of the sponge to these chambers, and

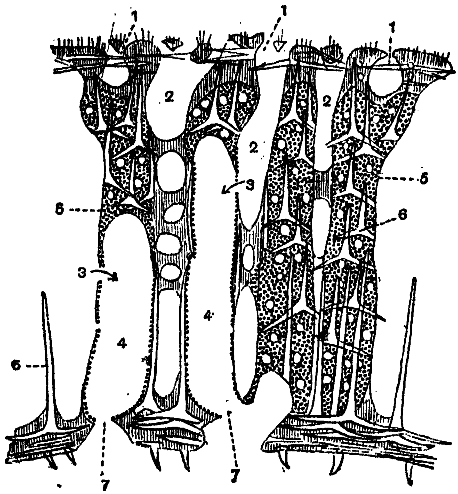


Fig. 8. Section of a portion of *Grantia*, a calcareous sponge. Highly magnified. (From Dendy.) 1, openings of inhalent canals; 2, inhalent canal; 3, openings of inhalent canals into flagellated chamber; 4, flagellated chamber; 5, collar cells; 6, spicules; 7, exhalent opening of flagellated chamber.

others, the *excurrent* or *exhalent* canals, may lead from the chambers and open into the gastral cavity. Further complications, such as branching of the canals, may occur. The thick wall of these more complex sponges is formed mainly of the gelatinous layer.

In a sponge consisting of a single individual, the form depends mainly on the relative rates of growth in different directions, and may be cylindrical, vase-like, globular, discoidal, etc. In a compound sponge the form depends also on the way in which the young individuals of the colony are attached to the parent, and in addition, on their remaining free or becoming fused together; in the latter case the individuals of the colony are frequently distinguishable by their oscula only; when the individuals remain free, arborescent or bushy colonies may result (fig. 12); if they become fused, the sponge may be fan-shaped, funnel-shaped, cup-like, tubular, mushroom-shaped, massive, encrusting, etc.

Nearly all sponges are attached to some foreign object—generally by the base of the sponge, but in forms which are fixed in the mud, especially deep-sea forms of the Hexactinellida, and in some Tetraxonida, this fixation is by means of a root-tuft or rope of long spicules.

In nearly all sponges there is a skeleton, which serves to support the canals and chambers and also for protection. This skeleton may consist of fibres of a horny substance, similar to silk in composition, and known as *spongin*; or of mineral particles, termed *spicules* (fig. 8, 6), composed of carbonate of lime or of colloid silica; or it may consist of both siliceous spicules and spongin. Those forms only which have either a siliceous or calcareous skeleton are definitely known as fossils. Each spicule consists of a number of rays or arms, coming off from a centre, which is the point where the formation of the spicule commenced. In some groups, as for instance in the Monaxonida and Tetraxonida, the spicules are not united or are joined by spongin only; but in others they are fused together or interlocked so as to form a complete scaffolding, and

generally it is in these only that the external form of the sponge has been preserved in the fossil state. In most siliceous sponges, two kinds of spicules may be distinguished, the *skeletal-spicules* or *megascleres* which build the main part of the skeleton, and the *flesh-spicules* or *microscleres* which are smaller and isolated and are seldom preserved as fossils. In the axis of each spicule there is a canal known as the *axial canal* (fig. 9, *c*), which in the living sponge is occupied by a thread of organic matter; this is the first part of the spicule to be formed, the mineral matter being subsequently deposited around it.

The spicules of recent siliceous sponges are characterised by the glassy appearance of their surface, and by the silica being colloidal, isotropic, and soluble in heated caustic potash. But in the fossil state the spicules have generally undergone considerable change; occasionally their silica is still colloidal but the surface has no longer the glassy appearance, and the axial canal is frequently filled with secondary silica in a crystalline or crypto-crystalline condition, and is consequently easily distinguished by the aid of polarised light when the spicule itself still remains colloidal. Generally, however, the spicule has become crystalline or crypto-crystalline, and in such cases the axial canal can rarely be detected since it is filled with material in the same condition. Sometimes the silica of the spicules has been entirely removed, a hollow cast only remaining; in other cases it is replaced by another mineral, as for instance by calcite in the sponges from the Lower Chalk of Folkestone, by iron pyrites in *Protospongia* from the Menevian Beds of St David's, by iron peroxide in the sponges of the Upper Chalk of the south of England, and by glauconite in some from the Upper Greensand. Obviously then, the colloidal silica of recent sponges is

anything but a stable substance, thus differing widely from crystalline and crypto-crystalline silica.

The spicules of the calcareous sponges are usually smaller than those of the siliceous forms, and their material is not in an isotropic state, but each spicule possesses the optical characters of a crystal of calcite; consequently in polarised light these spicules are readily distinguished from unaltered siliceous forms, which appear dark between crossed Nicol's prisms. Then again the fossil calcareous spicules have undergone much less chemical change than the siliceous ones; generally they are still composed of carbonate of lime, for it is only in rare cases that this is replaced by silica. The external form of the individual calcareous spicules is, however, often less well preserved than in the case of siliceous spicules.

The forms of sponge spicules, both megascleres and microscleres, are very varied, but they can be shown to be modifications of a small number of types or fundamental forms. The spicules, on account of the constancy of their characters, are of great importance in the classification of sponges.

The canal-system is indicated in the skeleton of both recent and fossil forms by spaces in the framework of spicules or spongin, but these spaces represent only the larger canals, the smaller existing in the soft parts alone.

Reproduction in the sponges takes place by budding and by the production of ova and spermatozoa.

The sponges may be divided into three classes:—(1) Hexactinellida, (2) Demospongiæ, (3) Calcarea. The first and second are sometimes grouped together as the Non-Calcarea.

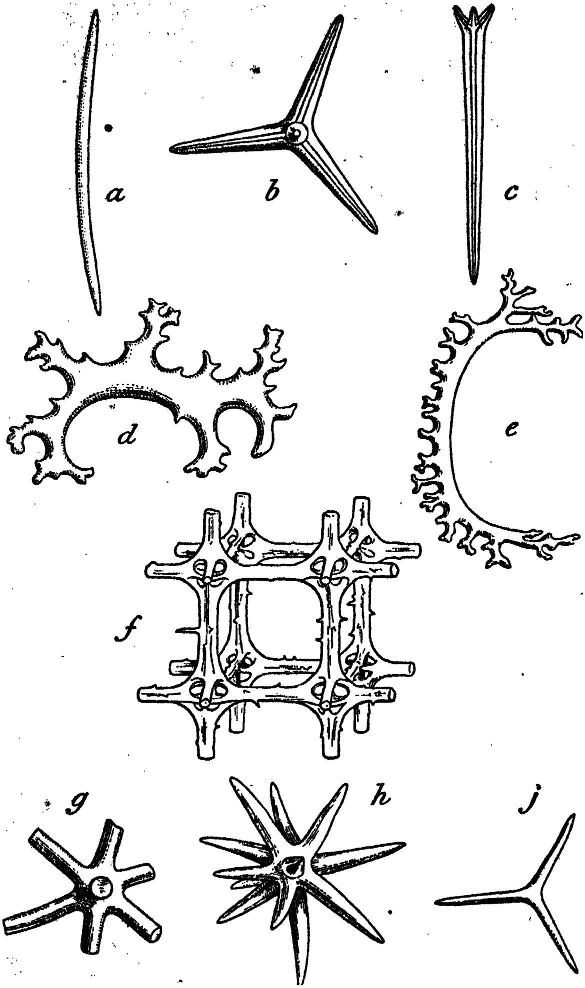


Fig. 9. **Sponge spicules (skeletal).** *a*, monaxonid, *Halichondria panicea*, Recent. *b*, tetraxonid (calthrops), *Pachastrella*, Upper Greensand. *c*, tetraxonid (triæne), *Geodites*, Eocene. *d*, lithistid, *Scytalia radiciformis*, Chalk. *e*, lithistid, *Seliscothon mantelli*. *f*, hexactinellid, *Cœloptychium agaricoides*, Chalk. *g*, octactinellid, *Astræospongia*, Silurian. *h*, heteractinellid, *Asteractinella expansa*, Carboniferous, *j*, calcisponge, *Grantia compressa*, Recent. All magnified.

CLASS I. HEXACTINELLIDA

The spicules in the Hexactinellida (fig. 9, *f*) consist of three axes crossing at right angles to one another; in primary forms there are consequently six rays of equal length proceeding from a centre. Each ray is traversed by an axial canal, and these unite at the point of junction of the six rays. Various modifications are produced by some of the rays being longer or shorter than the others, or almost absent; and also by the branching of the rays and the occurrence of spines, knobs, etc. The spicules may remain free or they may be fused with one another by a deposit of secondary silica, but they are never united by spongin. When spicules with equal rays are united end to end, skeleton-cubes are formed, each cube consisting of eight spicules (fig. 9, *f*). Flesh-spicules are abundant, but are seldom found fossil. Some of the spicules form a layer near the external surface of the sponge for the support of the dermal membrane; others form a similar layer near the internal surface; the spicules which constitute the main part of the skeleton occur in the middle of the sponge-wall and serve to support the canals and flagellated chambers. The spicules which form the root-tuft by which many Hexactinellids are fixed, are long and thread-like. The walls, as a rule, are thin and the canal-system is usually simple.

The earliest form is *Protospongia* from the Menevian Beds of St David's; *Hyalostelia* is found in the Tremadoc, and also occurs in the Ordovician, Silurian, and Carboniferous. In the Silurian the genera *Dictyophyton* and *Phormosella* are present. Hexactinellids are not known in the Permian and Trias, but they become abundant in the Jurassic, especially in the upper part, and also in the Cretaceous; they are rare in the Tertiary.

Protospongia (fig. 10). Form unknown but probably cup-shaped. Spicules cruciform owing to the reduction of one axis, and arranged in a quadrate manner, the larger forming a framework, which contains the smaller spicules of two or three sizes, arranged in the same regular way, so that the larger squares enclose four or five series of smaller ones. The spicules were either free or probably partly fused together. Menevian Beds and Lingula Flags. Ex. *P. fenestrata.*

Craticularia. Cup-shaped, funnel-shaped, or cylindrical; simple or branching. On both the inner and outer surfaces of the wall are circular or oval canal-openings, which are arranged in vertical and transverse rows crossing each other at right angles. Canals straight, terminating blindly. Inferior Oolite to Upper Chalk (perhaps also Miocene). Ex. *C. fittoni*, Chalk.

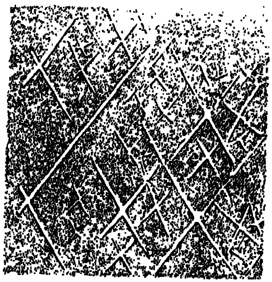


Fig. 10. *Protospongia fenestrata*, Menevian Beds, St David's. ×3⅔. (After Hinde.) The original is in the British Museum. Owing to the cleavage of the rock the angles of the spicules are distorted.

Ventriculites. Simple, form variable, but usually cup-shaped, funnel-shaped, or cylindrical. Central cavity large and deep. Walls folded so as to form a series of vertical grooves and ridges; the grooves are divided by transverse extensions of the wall into oval or elongate openings. Canal-system well developed; the radial canals are large and start from the central cavity, but end before reaching the outer surface; others start from the outer surface and end before reaching the central cavity. Spicules six-rayed and fused with one another so as to form a mesh-work. The node where the axes cross is hollow, having the form of a negative octahedron,

the central part of each face of which is absent; the axial canals cross in the centre of the octahedral space. The sponge was provided with a root consisting of siliceous fibres. Chalk. Ex. *V. radiatus*, *V. impressus*.

Plocoscyphia. Sponge formed of thin-walled tubes and laminæ which anastomose, forming an irregular or rounded mass. Small, close-set openings of canals on the outer surface. Canal-system imperfect. Upper Cretaceous. Ex. *P. fenestrata*, Upper Greensand and Chalk Marl.

CLASS II. DEMOSPONGIÆ

The skeleton consists of siliceous spicules, or of spongin, or of both spicules and spongin. In some forms there is little or no spongin, but in others the entire skeleton consists of spongin with no siliceous spicules; between these extremes there is a complete passage. The spicules are never of the hexactinellid type. In some few cases both spicules and spongin are absent.

ORDER 1. MYXOSPONGIDA. Sponges with no skeleton or occasionally with a few isolated spicules. Not known in the fossil state.

ORDER 2. CERATOSA. Sponges with a skeleton composed of a fibrous network of spongin. This Order includes the ordinary bath sponges, etc., and is unknown in the fossil state.

ORDER 3. MONAXONIDA. The skeleton is formed of spongin and spicules in varying proportions. The spicules (fig. 9, *a*) consist of a single rod or axis, which may be straight or curved, and with sharp or blunt ends; each spicule may consist of two rays or of one ray only. In the former the two ends of the spicule are alike and there is a small swelling of the axial canal at the centre of the spicule where growth commenced; in the latter the two

ends are dissimilar and the swelling in the axial canal is at one end of the spicule, and growth went on in one direction only. Microscleres or flesh-spicules may also occur but are often absent. Since in this Order the spicules are only united by spongin or other decomposable material, it is extremely rare to find the form of the sponge preserved fossil; usually, detached spicules only occur.

The earliest representatives of the Monaxonida are found in the Silurian; the Order becomes more abundant in the Carboniferous, where the genus *Reniera* occurs. The freshwater form *Spongilla* is found in the Purbeck Beds of the south of England. A large number of Monaxonid sponges are still living.

ORDER 4. TETRAXONIDA. The spicules (fig. 9, *b*, *c*) consist of four rays given off from a common centre, the angle between the rays, when the end of one is taken as a central point, appearing to be 120°. The rays may be equal in length, when the spicule is termed a *calthrops* (fig. 9 *b*), or unequal; frequently one is very much elongated (fig. 9, *c*), and in such forms, known as *triænes*, the three shorter rays are placed near the surface of the sponge-wall and the longer ray is directed inwards. Sometimes the terminations of the rays are bifurcated. Spongin is either absent or occurs in minute quantities only, and since the spicules are not united, the Tetraxonids, like the Monaxonids, are seldom preserved in anything like a perfect condition as fossils. The oldest forms occur in the Carboniferous Limestone, where they are represented by the genera *Geodites* and *Pachastrella*; others are found in the Infra-Lias, the Cretaceous and Tertiary formations.

ORDER 5. LITHISTIDA. The Lithistids have thick stony walls and very variable external form. The spicules

(fig. 9, *d*, *e*) are stout and irregular in form, but sometimes show four rays; the extremities branch or expand, and by that means the spicules become firmly interlocked with one another, but do not fuse together. These irregular spicules (sometimes termed *desmas*) are formed by secondary silica being deposited on small spicules of the ordinary kind, which may be four-rayed or consist of a single axis. In addition to these irregular spicules there is generally a surface layer or cortex formed of triæne spicules like those in the Tetraxonids. Flesh-spicules are also present. Several different types of canal-system occur. The Lithistids are closely allied to the Tetraxonida, and are sometimes regarded as a division of that Order.

Owing to their solidity the Lithistids are preserved abundantly as fossils. They are rare in the Palæozoic; a few are found in the Upper Cambrian of Canada; in the Ordovician and Silurian *Astylospongia* occurs; in the Carboniferous *Doryderma*, etc. No forms belonging to this Order have been found in the Devonian, Permian, or Trias; they are numerous in the Jurassic, attain their maximum in the Cretaceous, and are scarce in the Tertiary.

Verruculina. Irregular, fan- or funnel-shaped, attached by a short stalk. Oscula placed on prominent elevations on the upper, and sometimes also on the under surface. Spicules small, interlacing and forming a fibrous network. Upper Cretaceous. Ex *macromammata* (=*reussi*), Upper Chalk.

Pachinion. Pear-, fig- or club-shaped, sometimes cylindrical, tapering at its lower part to a short stem. Central cavity large and deep, with vertical canals opening into its base. Wall formed of anastomosing fibres, between which are irregular spaces—there are no distinct canals; fibres formed of large spicules, branched and interlaced. There is also a surface layer composed of small spicules. Chalk. Ex. *P. scriptum*, Upper Chalk.

Scytalia. Simple, or formed of two or more individuals growing close together; cylindrical or club-shaped, with a thick wall and a cylindrical stem. Central cavity tube-like, long, continued at its base by several vertical canals; numerous radial canals open into the central cavity and taper toward the external surface. Spicules branching, with root-like prolongations. Chalk. Ex. *S. radiciformis.*

Seliscothon. Mushroom-like, consisting of a flat or concave, circular, plate-like body, and a rounded tapering stem. The circular body has rounded or oblique edges, and numerous, small, rounded oscula on the upper surface; it is formed of fine vertical radiating lamellæ, separated by spaces crossed by fibres—these spaces forming the canal-system. Spicules fine, branching irregularly, with bifurcating extremities, and covered with tubercles or spines. Chalk. Ex. *S. planum.*

Doryderma. Cylindrical, pear-shaped, sometimes branching. There are parallel vertical canals opening at the summit of the sponge, and smaller radial canals extending from the surface towards the centre. Spicules large, of various forms; also a surface layer formed of slender trifid spicules. Carboniferous and Cretaceous. Ex. *D. benetti*, Upper Greensand.

Siphonia (fig. 11). Pear-, apple- or fig-shaped, provided with a long or short stalk, which is given off from the broad end of the body and terminates in rootlets. The incurrent canals are small, slightly curved, and extend radially from the centre of the sponge to the surface. The excurrent canals are larger, and are arranged parallel with the surface of the sponge, extending from the base to the summit, where they open into the deep central cavity by means of a series of parallel ostia. The skeletal-spicules possess four rays with bifurcated and expanded extremities, by means of which they are interlocked. Upper Greensand to Upper Chalk. Ex. *S. tulipa*, Upper Greensand.

Hallirhoa. Like *Siphonia* but with the sides divided into lobes. Upper Greensand. Ex. *H. costata.*

ORDER 6. OCTACTINELLIDA. The spicules (fig. 9, *g*), consist of eight rays, six of which are in one plane diverging at equal angles, while the other two are at right

angles to this plane, forming a vertical axis. Frequently, however, the vertical axis is only slightly developed or altogether absent. The spicules are not united. The only genus is *Astræospongia*, found in the Silurian and Devonian.

Order 7. Heteractinellida. The spicules are unusually large (fig. 9, *h*), the number of rays varying from six to thirty. The body spicules are not fused, but there is a surface layer in which the spicules are interwoven and

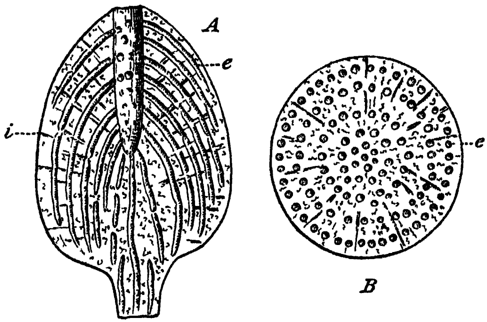


Fig. 11. *Siphonia tulipa*, Upper Greensand, Warminster. A, vertical section. B, horizontal section. *e*, excurrent canals; *i*, incurrent canals. × ⅔.

more or less fused. The only genera are *Tholiasterella* and *Asteractinella*, found in the Carboniferous rocks of Ayrshire.

CLASS III. CALCAREA

The skeleton consists of spicules composed of carbonate of lime in the condition of calcite. The spicules are usually much smaller and less varied in form than those of the siliceous sponges, and cannot be separated into megascleres and microscleres. There are three kinds, the

simple uniaxial, the three-rayed—with the rays in one plane (fig. 9, *j*), and the four-rayed; they are sometimes fused with one another, but often are either arranged close together so as to form fibres, or are loosely distributed. Spongin is never present. The earliest British forms of the Calcarea occur in the Carboniferous rocks of Fifeshire.

Peronidella. Cylindrical, simple or branched; central cavity tubular and extending from the summit to the base of the sponge. Walls thick and with no definite canals, but having irregular spaces between the spicular fibres. Spicules three- or four-rayed, forming anastomosing fibres. Carboniferous (possibly also Devonian) to Cretaceous; most abundant in the Jurassic and Cretaceous. Ex. *P. pistilliformis*, Great Oolite and Cornbrash.

Corynella. Form similar to *Peronidella*. Radial excurrent canals open into the central cavity, which often does not extend to the base of the sponge, but is continued downwards by vertical canals. Incurrent canals fine, directed obliquely downward. Osculum usually with radial furrows. Jurassic and Cretaceous (? Trias). Ex. *C. foraminosa*, Lower Greensand.

Holcospongia. Simple or compound: individuals usually spherical, hemispherical, or club-shaped; their summits rounded, with a central area in which a number of excurrent canals open, and from which furrows extend down the sides of the sponge. Spicules large and three-rayed, and some also filiform; and a surface layer of three-rayed spicules, of various sizes, felted together. Inferior Oolite to Cretaceous. Ex. *H. polita*, Corallian.

Rhaphidonema. Cup- or funnel-shaped or leaf-like, usually with definite canals. Oscula on either the inner or the outer surface. Spicules of three rays, one of which is but slightly developed. On one (or sometimes both) surfaces is a thin, compact or finely porous layer of spicules. Trias to Cretaceous. Ex. *R. macropora*, Lower Greensand.

Barroisia (fig. 12). Usually compound and bushy. Individuals cylindrical, each divided into a series of chambers by transverse partitions, which have a central circular opening, through which

a tube usually passes. Canals simple, numerous, minute. Spicules slender, three-rayed; also a surface layer of larger spicules. Lower Greensand to Chalk. Ex. *B. anastomans*, Lower Greensand.

Porosphæra. Small simple sponges, commonly more or less spherical, but sometimes pear-, thimble-, or melon-shaped; often free, but sometimes attached to foreign bodies. Numerous, simple, straight, radiating canals open at the surface by minute apertures. Spicules with four rays, of which three are short and blunt and fused to the rays of adjoining spicules, whilst the fourth ray is longer and tapering. A surface layer (not often preserved) consists of a mixture of minute three- and four-rayed spicules and simple rods. Upper Cretaceous. Ex. *P. globularis*, Chalk.

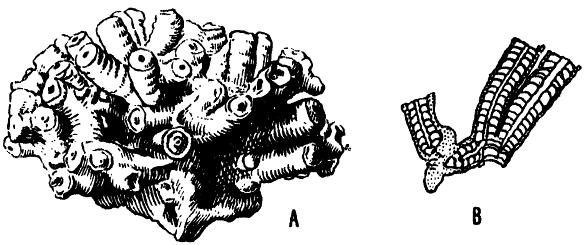


Fig. 12. *Barroisia anastomans*, Lower Greensand, Faringdon. A, colony. B, vertical section of three individuals of a colony. × $\frac{3}{4}$.

Distribution of the Porifera.

The Sponges are all aquatic, and with the exception of the Monaxonid genus *Spongilla* and its allies, all marine. They are found in the seas of all parts of the world and are more numerous between the shore-line and 200 fathoms than at greater depths; many of the genera have a very wide distribution. All the Orders except the Octactinellida and the Heteractinellida have living representatives. The Monaxonids are abundant between the shore-line and 200 fathoms, and gradually decrease in numbers beyond that limit. The Tetraxonids are also

common in water of less depth than 200 fathoms, but extend down to 2000 fathoms. The Lithistids range from $7\frac{1}{2}$ to 1075 fathoms, and are most abundant between 100 and 150 fathoms. The Hexactinellids occur in deeper water than the Lithistids, being found down to a depth of 2900 fathoms; but they are abundant between 100 and 200 fathoms, and again between 300 and 700 fathoms. The Calcarea are mainly shallow water forms.

The fossil forms are comparatively rare in the Palæozoic rocks until we reach the Carboniferous; and throughout the geological formations they are much less abundant in argillaceous than in calcareous and arenaceous rocks. Sponges are first found in the Lower Cambrian rocks; the earliest British form is *Protospongia* from the Menevian Beds and Lingula Flags; in the Tremadoc the Hexactinellid genus *Hyalostelia* occurs, ranging onwards as far as the Chalk. In the Ordovician we have in the Llandeilo Beds the first appearance of *Ischadites*[1], associated with *Hyalostelia*; in the Bala Beds we meet with *Astylospongia*. The most abundant Silurian form is *Ischadites*; *Astræospongia, Phormosella*, and *Hyalostelia* also occur. Sponges are rare in the Devonian, but *Astræospongia, Sphærospongia*[1], and *Receptaculites*[1] have been recorded. In the Carboniferous rocks sponges become much more common, the siliceous spicules often forming thick beds of chert: the Monaxonids are represented by *Reniera*, the Tetraxonids by *Geodites*, the Lithistids by *Doryderma*, the Hexactinellids by *Hyalostelia*, and the Heteractinellids by

[1] The sponge-character of the Silurian and Devonian genera *Ischadites*, *Receptaculites*, and *Sphærospongia*, which have been placed by some authors in the Hexactinellida, is now disputed; if they are sponges it is probable that they belong to the Calcarea, since their skeleton appears to have consisted originally of carbonate of lime.

Tholiasterella and *Asteractinella*. Sponges appear to be absent in the Permian; and they are rare in the Trias, except in the St Cassian Beds of the Tyrol, where the Calcarea are numerous.

In the Jurassic, sponges are extremely abundant; the only Monaxonid is *Spongilla* from the Purbeck Beds; Lithistids and Hexactinellids although common in Germany and Switzerland are comparatively rare in England; the first group is represented by *Platychonia*, the second by *Craticularia*, *Verrucocœlia*, etc.; the Calcarea are numerous in this country as well as in France and Germany, common genera being *Peronidella*, *Corynella*, and *Holcospongia*. The occurrence of Hexactinellids in the Inferior Oolite is noteworthy, since other evidence shows that that deposit was laid down in shallow water, but at the present day Hexactinellids are characteristic of deep water.

Sponges are more abundant in the Cretaceous than in any other system. In England they are found chiefly at four horizons:—(1) in the Lower Greensand of Faringdon, Upware, Kent, and Surrey, where the Calcarea are much better represented than the other groups, *Peronidella*, *Barroisia*, and *Rhaphidonema* being common forms: (2) in the Upper Greensand and Chloritic Marl of Warminster, Blackdown, Haldon, and the Isle of Wight, where the Lithistids (*e.g.* *Doryderma*, *Siphonia*, *Hallirhoa*) are very abundant, exceeding the Hexactinellids (*e.g.* *Craticularia*, *Plocoscyphia*, *Stauronema*); the Calcarea are also common in places: (3) in the Lower Chalk of the south of England, where we find *Siphonia*, *Craticularia*, *Stauronema*, *Plocoscyphia*, etc.; the Calcarea are rare: (4) in the Upper Chalk, where the siliceous sponges are very common; amongst the Lithistids the following occur:—

Seliscothon, Verruculina, Scytalia, Doryderma, and *Siphonia*; the Hexactinellids are represented by *Craticularia, Verrucocœlia, Guettardia, Ventriculites, Cephalites, Plocoscyphia,* and *Camerospongia*; the Calcarea are represented by *Porosphæra.* In the Tertiary formations detached spicules are sometimes abundant, but few perfect sponges have been found.

PHYLUM CŒLENTERA

Classes.		*Orders.*
1.	Hydrozoa	1. Gymnoblastea. 2. Calyptoblastea. 3. Graptolitoidea. 4. Hydrocorallina. 5. Stromatoporoidea. 6. Trachomedusæ (not fossil). 7. Narcomedusæ (not fossil). 8. Siphonophora (not fossil).
2.	Scyphozoa....................	1. Stauromedusæ (not fossil). 2. Peromedusæ (not fossil). 3. Cubomedusæ (not fossil). 4. Discomedusæ.
3.	Anthozoa or Actinozoa ...	1. Zoantharia. 2. Alcyonaria.
4.	Ctenophora (not fossil).	

THE Cœlentera include hydroids, jelly-fishes, sea-anemones, corals, and allied forms. The individuals are radially symmetrical, and have only one internal cavity, the *cœlenteron*, which opens to the exterior by the mouth. The body-wall consists of an outer layer of cells, the *ectoderm*, and an inner layer, the *endoderm*; between these is a gelatinous layer—usually quite thin, but in the jelly-fishes of considerable thickness. Stinging cells known as nematocysts or thread-cells are generally present in the ectoderm. The canal-system, so characteristic of the sponges, is absent.

This Phylum is divided into four classes, (1) Hydrozoa, (2) Scyphozoa, (3) Anthozoa or Actinozoa, (4) Ctenophora.

CLASS I. HYDROZOA

The simplest type of the Hydrozoa is the common fresh-water *Hydra.* In this the body has the form of an elongated sac, about a quarter of an inch in length, and is attached by one end, whilst at the other is the mouth surrounded by a row of long processes, called *tentacles.* The large undivided cavity in this sac, which opens into the hollow tentacles above, is the cœlenteron. The whole body is very contractile and constantly changing its shape. Reproduction may take place in three ways, (1) by the growth of buds, which ultimately separate from the parent, (2) sexually, by the production of ova and spermatozoa in the ectoderm, and (3), in rare cases, by fission.

Other Hydrozoa consist of a number of individuals (polyps or hydranths) similar to *Hydra*, but growing together as a colony (fig. 13); in such cases the cœlentera of all the individuals are placed in living communication with one another by means of a tube-like extension from the base of each polyp; this common connecting portion of the colony is called the *cœnosarc* (fig. 13, 5). Frequently the cœnosarc is much branched, giving rise to tree-like forms; it is usually attached to some foreign object by a horizontal branching portion.

In such hydroid colonies the polyps are asexual, and the reproductive elements are produced in another individual of a somewhat different character, known as a *medusa* or *gonophore*: this arises by budding from the hydroid (fig. 13, 9), and is often more or less bell-shaped, and may become detached from the colony, or it may be less perfectly developed and remain attached; at the inner edge of the bell is a shelf-like fold, the *velum.* The generative cells are of ectodermal origin, and from them the hydroid develops.

Hydra possesses no hard parts, but in other forms an external skeleton composed of chitin or of carbonate of lime is secreted; it commonly forms a tube-like sheath around the cœnosarc and is called the *perisarc* (fig. 13, 6). In one group the perisarc is produced at the base of each polyp into a cup-like structure or *hydrotheca* (fig. 13, 7), into which the polyp can retract. The gonophores may also be protected by a chitinous capsule called the *gonotheca* or *gonangium* (fig. 13, 10). The vertical branching part of the cœnosarc together with the perisarc around it, is called the *hydrocaulus*; the horizontal root-like portion and its perisarc form the *hydrorhiza*.

The principal characters which distinguish the Hydrozoa from the other Cœlenterates are: the cœlenteron being undivided by radial partitions or ridges; the absence of a digestive tract projecting into the cœlenteron; the usual occurrence of an asexual (hydroid) generation alternating with a sexual (medusoid) generation; the medusa having a velum; the ova and spermatozoa being derived from the ectoderm.

Nearly all the Hydrozoa are marine. They are divided into eight Orders, of which five occur fossil:—(1) Gymnoblastea, (2) Calyptoblastea, (3) Graptolitoidea, (4) Hydrocorallina, (5) Stromatoporoidea.

ORDER I. GYMNOBLASTEA

The Gymnoblastea have no hydrothecæ into which the polyps can retract; gonangia (gonothecæ) are also absent.

Well-known living forms are *Tubularia*, *Bougainvillea*, and *Hydractinia*. The last has been found fossil in Eocene and later deposits; it forms a crust over the shells of gasteropods, especially those tenanted by Hermit-crabs. The hard part of this crust is chitinous, or rarely cal-

careous, and consists of laminæ separated by irregular or cubical spaces and crossed by vertical pillars; on the surface are projecting spines. The soft parts form a layer over this skeleton, and consist of a sheet of ectoderm on the surface, and another sheet next the skeleton; between these are branching and anastomosing cœnosarcal tubes. The skeleton is secreted by the lower ectoderm. From the cœnosarc arise the polyps, which are placed on long vertical stalks and are of four kinds, (1) gastrozooids—the ordinary nutritive individuals, (2) blastostyles, which are individuals specially modified for bearing medusæ, (3) dactylozooids—individuals modified for catching prey and having short knob-like tentacles crowded with nematocysts, (4) tentacular polyps, which are very slender, without a mouth, and occur near the edge of the colony.

Parkeria, which is found in the Cambridge Greensand, probably belongs to this Order. A few other forms have been described from the Alpine Trias and the Jurassic of southern Europe.

ORDER II. CALYPTOBLASTEA

This Order is distinguished by the presence of hydrothecæ into which the polyps can completely retract, and by the possession of gonangia (gonothecæ). (Fig. 13, 7, 10.)

The arrangement of the polyps and hydrothecæ on the hydrocaulus varies considerably in different genera. Sometimes they are placed on stalks as in *Obelia* (fig. 13) and *Campanularia*; in many others they are sessile. They may be in rows or placed in various positions on the hydrocaulus. In *Plumularia, Aglaophenia,* etc., they form a single row; in *Sertularia,* etc., there are two rows placed on opposite sides of the branches. Sometimes the hydrothecæ are close together, but more usually they are separated.

In the Plumulariidæ there are, in addition to the ordinary polyps, others which are solid and tentacle-like;

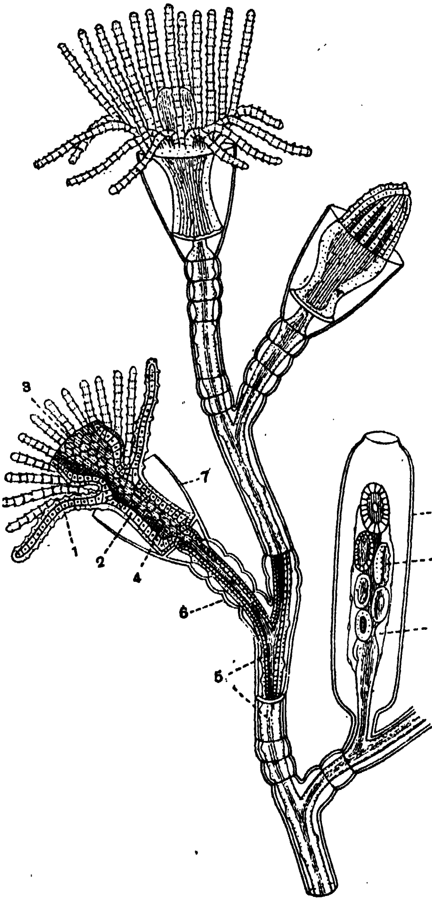


Fig. 13. Part of a branch of *Obelia*. Enlarged. To the left a portion is shown in section. (After Parker and Haswell.) 1, ectoderm; 2, endoderm; 3, mouth; 4, cœlenteron; 5, cœnosarc; 6, perisarc; 7, hydrotheca; 8, blastostyle, a mouthless polyp bearing medusa-buds; 9, medusa bud; 10, gonangium or gonotheca.

they are usually provided with nematocysts and are called *nematophores*; each one is placed in a hydrotheca.

Although the Calyptoblastea possess a well-developed chitinous skeleton, yet, with the exception of a form found in the Pleistocene, they are not definitely known to occur as fossils.

In the Lower Palæozoic, however, there are organisms, usually termed 'dendroid graptolites,' which present con-

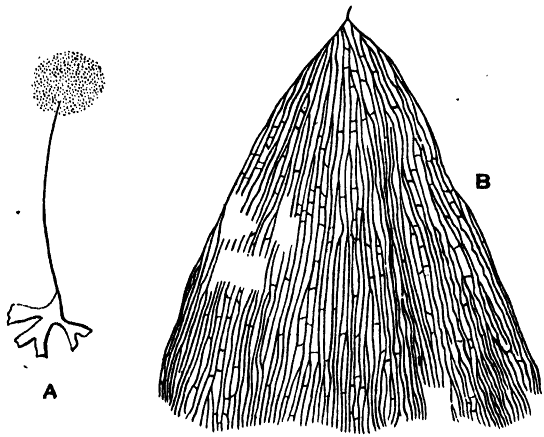


Fig. 14. *Dictyonema flabelliforme*, Upper Cambrian. (After Ruedemann.) A, young form with thread and disc for attachment. × 3. B, complete colony. × ⅔.

siderable resemblance to the Calyptoblastic hydroids, but are sometimes regarded as a division (Dendroidea) of the Graptolitoidea; the best known are *Dendrograptus*, *Ptilograptus*, *Dictyonema* (fig. 14), and *Callograptus*. These are usually much branched and tree-like, and some are fixed by a root-like structure, others by thread coming off from the point of the sicula (fig. 14 A). Transverse sections of *Dictyonema* and *Dendrograptus* show that some of the

branches consist of a group of tubes of various sizes, somewhat resembling in this respect the recent Calyptoblastean forms *Clathrozoon* and *Grammaria*. Those genera which possess a sicula and were suspended by a thread coming off from its pointed end appear to be closely related to the true graptolites.

Dictyonema (=*Dictyograptus*) (fig. 14) is found in the Cambrian, Ordovician and Silurian, and in the Devonian of North America, and has a fan- or funnel-shaped skeleton which consists of numerous radiating branches, placed nearly parallel with one another, and united by transverse fibres; a sicula is present. *Dendrograptus* occurs in the Upper Cambrian and Ordovician, *Callograptus* in the Arenig, and *Ptilograptus* ranges from the Arenig to the Ludlow Beds.

ORDER III. GRAPTOLITOIDEA

The graptolites are found only in the Lower Palæozoic rocks, where, owing to their abundance and to the limited range in time of both genera and species, combined with their wide geographical distribution, they are of great importance to the stratigraphical geologist. They occur most commonly in argillaceous rocks, especially in black carbonaceous shales, whilst they are relatively rare in sandstones and limestones. The graptolites were compound animals, and the soft parts were protected by a skeleton of chitin which shows a general resemblance to that found in the Calyptoblastea, *e.g. Sertularia* and *Plumularia*. But the original material of the skeleton is seldom preserved unaltered; in some cases it has been replaced by iron pyrites, but usually it has become carbonised.

The entire skeleton of the graptolite is termed the *polypary*; this in an unbranched form like *Monograptus*

consists of a tubular part known as the common canal (fig. 15 b, c), which extends nearly the whole length of the animal, the wall being termed the *periderm* or perisarc. From one side of the common canal small tooth-like projections are given off; these are the *hydrothecæ* (fig. 15, b, *h*), each of which is hollow and opens on the one hand into the common canal and on the other to the exterior; the latter aperture, known as the *mouth* (*m*) of the hydrotheca, is frequently circular, but sometimes quadrangular or slit-

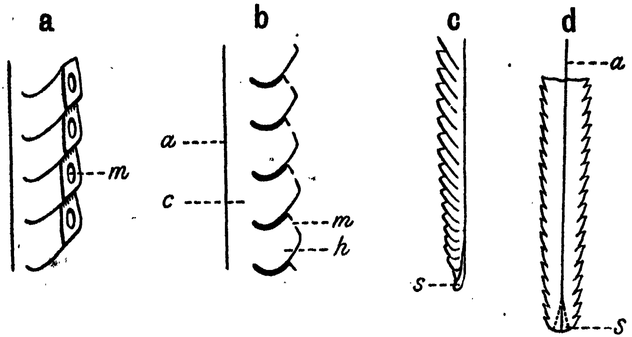


Fig. 15. a, Portion of *Monograptus personatus*. b, diagrammatic vertical section of the same. c, *Monograptus colonus*, Coniston Grits, with sicula (*s*). d, *Diplograptus foliaceus*, Llandeilo Beds, with virgula (*a*), and the position of the embedded sicula (*s*) indicated. All enlarged. *a*, position of virgula in wall of b; *c*, common canal; *h*, hydrotheca; *m*, mouth of hydrotheca; *s*, sicula.

like. Embedded in the periderm on the side opposite to the row of hydrothecæ is a chitinous thread or rod, termed the *virgula* (fig. 15 b, *a*). In some species of *Monograptus* the virgula projects beyond the distal[1] end of the common canal. At the proximal end of the polypary there is a

[1] The proximal end is that next the sicula and is the part which is formed first; the distal end is furthest from the sicula and is formed last. The side of the graptolite on which the hydrothecæ occur is spoken of as the *ventral*, and the opposite side as the *dorsal*.

small conical body, termed the *sicula* (fig. 15, c, *s*), which will be described more fully below (p. 63).

The soft parts of the graptolites are unknown, but from comparison with living hydroids which have a similar skeleton, we may consider it probable that each hydrotheca lodged an individual polyp, and that these were connected by means of the cœnosarc in the common canal.

In the form just described (*Monograptus*) the polypary is always simple, but in many genera it consists of two or

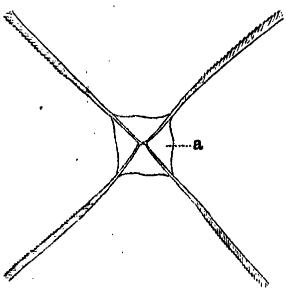


Fig. 16.

Fig. 17.

Fig. 16. *Tetragraptus headi*, Arenig Rocks. *a*, central disc. × ½.
Fig. 17. *Climacograptus parvus*, Ordovician. With vesicle at end of virgula. (After Ruedemann.) × 1½.

more branches or stipes. When there are several radiating branches their proximal parts are sometimes enclosed in a horny sheath, termed the *central disc*, as in some species of *Tetragraptus* (fig. 16). In those genera which have two branches (fig. 20), the angle between the two is termed the *angle of divergence*; it is measured from the hydrothecal side of each branch. In some graptolites (*e.g. Mono-*

graptus, fig. 15 c) there is only a single row of hydrothecæ, such forms are said to be *uniserial*; others (*e.g. Diplograptus*, fig. 15 d) possess two rows on opposite sides of the polypary—these are the *biserial* forms, and they may have a single common canal as in *Retiolites*, or there may be two canals separated by a septum, as in *Climacograptus*: in many forms of *Diplograptus* there is only one common canal, but others possess an incomplete septum which, to some extent, divides the canal into two parts. In *Dicranograptus* the proximal part of the polypary is biserial, whilst the distal part consists of two uniserial branches. In *Dimorphograptus*, on the other hand, the proximal part is uniserial and the distal part biserial; this genus therefore serves to connect the biserial *Diplograptus* with the uniserial *Monograptus*.

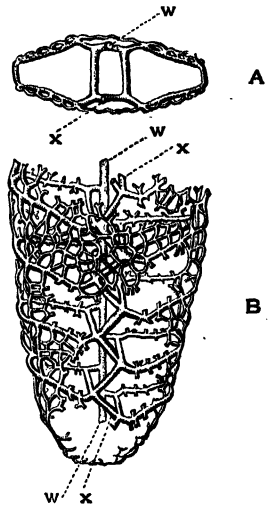


Fig. 18 *Retiolites geinitzi*, Silurian. A, section across polypary. B, proximal end of polypary with the outer layer removed. Enlarged (after Holm). *w*, *x*, rods in the network formerly regarded as virgulæ.

The hydrothecæ vary considerably in form in different genera, and sometimes even in different species of the same genus; but in any one species, with the exception of a few of the earlier hydrothecæ, they are usually similar in form, but diminish in size towards the proximal end of the polypary; they may resemble the sicula in shape, or they may be tubular, prismatic, conical, straight or coiled (*Monograptus lobiferus*). They may be in contact throughout their entire length (*Phyllograptus*), at their bases only (*Nemagraptus*), or, in a few

cases, entirely separate (*Rastrites*). Frequently they are provided with one or more spines near the mouth. In most graptolites the hydrothecæ communicate freely with the common canal, and in this respect differ from living hydroids, in which there is a constriction or an imperfect diaphragm at the base of each hydrotheca, separating it from the common canal (fig. 13); but some specimens of *Didymograptus* and *Tetragraptus* seem to show evidence of a septum between each hydrotheca and the common canal.

A microscopic examination of thin sections of *Monograptus* shows that the periderm consists of three layers, the external and internal layers being much thinner than the middle layer. In a few graptolites the middle layer of the periderm is more or less extensively perforated and may become reticulate; this modification is especially noteworthy in *Retiolites* in which the middle layer is reduced to a network of fibres (fig. 18) whilst the inner and outer layers are very thin.

In the uniserial genera the virgula, when present, is found in the periderm opposite the row of hydrothecæ, but in the biserial forms it is central (fig. 15 d, *a*), being situated either in the middle of the common canal, as in some forms of *Diplograptus*, or in the septum separating the two canals, as in *Climacograptus*; in such biserial forms the virgula is commonly enclosed in a tube-like covering. In several of the earlier genera (*Didymograptus, Phyllograptus, Tetragraptus, Dichograptus*) the virgula is not found in the wall of the common canal, but is represented by a thread which projects from the pointed end of the sicula and commonly ends in a chitinous disc by which the graptolite was attached (fig. 21).

The position of the sicula, in relation to the rest of the

polypary, varies in different genera, and depends on the directions in which the hydrothecæ grow. In *Monograptus* the sicula is united to the dorsal surface of the polypary, the pointed end being directed distally (fig. 15 c, *s*). In *Diplograptus* it has a similar position but is more or less completely enclosed between the hydrothecæ (fig. 15 d, *s*). In *Didymograptus* its broad end only is united to the two branches of the polypary, the pointed end being directed proximally (fig. 20, *s*). In *Dicellograptus* it projects like a spine between the two branches.

The appearance of even the same species of graptolite varies considerably according to its mode of preservation. Frequently it is flattened to a film, and when this is the case we may get a side view, a front view showing the mouths of the hydrothecæ, or a back view; in the two latter cases the margins will be parallel. But when the original material has been replaced by iron pyrites, or when the graptolite is preserved in a limestone, the natural form of the polypary is often retained.

No medusoid form is known in the graptolites; but sac-like bodies, which may be gonangia, are sometimes present. In a few biserial graptolites (fig. 19) such bodies have been found attached to the polypary; they are not joined to the hydrothecæ, but come off at right angles to them along the middle line of the sides of the polypary, but since no siculæ have been found in or near these sacs their nature and function must be regarded as uncertain. In other cases, however, sacs or vesicles containing siculæ have been seen near the distal extremity of the virgula (fig. 23), and it is probable that these are of the nature of gonangia (fig. 13, 10).

The earliest stage in the development of the graptolite at present known is the *sicula* (fig. 22 A); this probably

arises within the sac-like bodies mentioned above. The sicula is usually more or less clearly exposed at the proximal end of the polypary (figs. 15 c, 20 *s*); it is a hollow cone (fig. 22 A) open at the base, and consists of two parts—the pointed or apical end with a thin wall (*b*), and the broader or apertural part with a thick wall marked

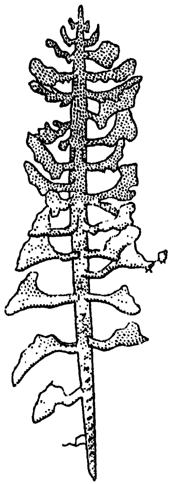


Fig. 19.

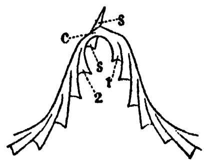


Fig. 20.

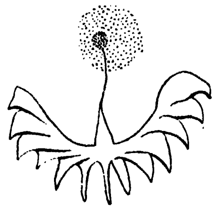


Fig. 21.

Fig. 19. *Diplograptus* with sacs resembling gonangia. (After Hall.) Natural size.

Fig. 20. *Didymograptus* v-*fractus*, Arenig Beds. Early part of the polypary. (After Elles.) *s*, sicula; *c*, crossing-canal; 1, first hydrotheca; 2, second hydrotheca. ×5.

Fig. 21. *Tetragraptus similis*, Lower Ordovician. Young form with virgula and disc. (After Ruedemann.) ×4.

with lines of growth (*a*). The pointed part was probably the covering of the embryo, and the broad part a later growth. The apical end of the sicula is prolonged as a thread forming the virgula. A spine-like projection is sometimes found at the apertural end of the sicula (fig.

22 A, c), but has no connection with the virgula. In the development of *Didymograptus* a bud is formed on one side of the sicula and from this arise (1) the first hydrotheca (fig. 20, 1) and (2) a tubular body known as the crossing-canal (c); the latter grows across the sicula and gives rise to the second hydrotheca (2) which is on the

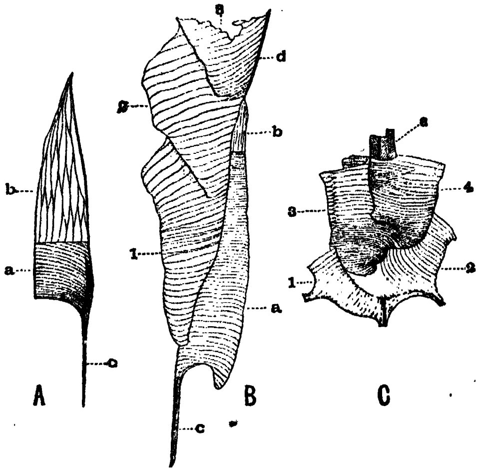


Fig. 22. Early stages of *Monograptus* and *Diplograptus*. (After Wiman.) Enlarged.

A. Sicula of *Monograptus*, from the Silurian of Gothland. *a*, thick-walled part with lines of growth; *b*, the earliest part with a thin wall; *c*, spine-like projection from the apertural end of the sicula.

B. *Monograptus* (same locality) with three hydrothecæ developed. 1, 2, 3, first, second, and third hydrothecæ; *a*, *b*, sicula; *c*, spine-like projection; *d*, virgula.

C. *Diplograptus* from Bornholm, with four hydrothecæ developed. 1, 2, 3, 4, first, second, third, and fourth hydrothecæ; *a*, sicula.

side opposite to the first hydrotheca. From each of these two hydrothecæ a stipe or branch is developed, owing to the fact that each hydrotheca gives rise by budding to another hydrotheca and in this way two continuous linear

series are formed. More complex branching (as in *Tetragraptus*, *Dichograptus*) is produced when one hydrotheca buds off two hydrothecæ instead of one. In *Diplograptus* (fig. 22 C) the development is similar to that of *Didymograptus* but the crossing-canal is reduced in size and the hydrothecæ grow up the virgula instead of in the direction of the apertural end of the sicula; also the hydrothecæ are budded off on either side alternately, so that the second hydrotheca (2) is on the side opposite to the first (1), and the third (3), which is budded from the second, is on the same side as the first and overlies it. This alternate arrangement may continue throughout the development of the polypary, but frequently a septum appears between the two rows of hydrothecæ, and thenceforward each hydrotheca arises from the preceding one on the same side. In *Monograptus* the hydrothecæ (fig. 22 B) arise on one side only of the sicula.

Whilst each polypary consists of a colony of individual polyps there is evidence which seems to indicate that in some biserial graptolites a number of polyparies were grouped together to form larger colonies. Thus Ruedemann has described specimens of *Diplograptus foliaceus* (fig. 23), from the Utica Slate (Ordovician) of New York, which consist of a number of individuals radiating from a centre where they unite by the distal prolongations of their virgulas; at the point of union there is a small, nearly square, chitinous sheath which is similar in appearance to the central disc of *Tetragraptus*; below this is a larger quadrate body, apparently vesicular, which may have been either a float (pneumatocyst) or an organ of fixation. Around the small disc are from four to eight globular vesicles, which Ruedemann considers to be gonangia, since they contain siculæ; the siculæ sometimes pass out and

develop into fresh colonies, but in other cases they remain attached to the parent, and, by the growth of the virgula, extend outwards, and subsequently hydrothecæ arise in the usual way. In some other species of *Diplograptus* (*D. vesiculosus*, etc.) and in *Climacograptus* (fig. 17) a single vesicle is sometimes found at the distal end of the virgula. A vesicle may also occur at the proximal end of the polypary, but its function is unknown.

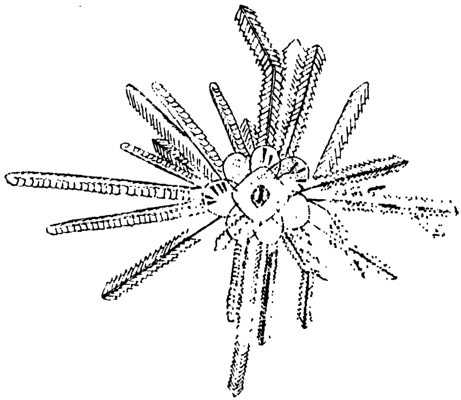


Fig. 23. *Diplograptus foliaceus*, from the Utica Slate, New York. × ⅔. (After Ruedemann.)

Owing to the fact that the soft parts of the graptolites are entirely unknown it is difficult to speak of their affinities with any degree of certainty. It seems probable, however, that they belong to the Hydrozoa; Allman and others consider them to be related to the Calyptoblastea, especially to such forms as *Sertularia* and *Plumularia*, with which they agree in the general characters of the hydrothecæ and common canal, and perhaps also in the possession of gonangia. But they differ in some important respects from the Calyptoblastea, *e.g.* in possessing a virgula and sicula,

in the diminution in size of the hydrothecæ towards the proximal end of the polypary, in the hydrothecæ being nearly always in contact, and in the free communication which exists in most cases between the hydrothecæ and the common canal; their development is also different—in the graptolites each hydrotheca is budded off from another hydrotheca, but in the Calyptoblastea the new polyps are budded off from the cœnosarc. Further, the graptolites never form the much-branched tree-like colonies which occur so commonly in recent hydroids, and the graptolites are never firmly fixed by any root-like structure corresponding to the hydrorhiza. On the other hand the dendroid graptolites (p. 57), to which the true graptolites appear to be related, do form much-branched colonies with, in some cases, a root-like hydrorhiza.

Since the graptolites do not possess any root-like structure (hydrorhiza) such as is found in many living hydroids it is not likely they were sessile animals living on the sea-floor; further, if that had been their mode of life some specimens would almost certainly be found in a vertical position crossing the planes of lamination, but that is not the case, for the graptolites are found lying flat on the lamination planes as if they had sunk slowly to the bottom in quiet water. The remarkably wide geographical distribution of the species can only be accounted for if the graptolites lived attached to floating sea-weeds or were free-swimming animals. There is evidence to show that many graptolites were fixed to some foreign object by means of the thread which comes off from the point of the sicula and ends in a chitinous disc (fig. 21); it is possible that some of the later biserial graptolites were free-swimming animals, since the vesicle found at the centre of the radiating colonies (fig. 23) and at the distal end of the

single stipes (fig. 17) may have served as a float; also the perforate or reticulate structure of the wall of some biserial forms (fig. 18) appears to be an adaptation for a floating mode of life. The much greater abundance of graptolites in thin, fine-grained, carbonaceous shales than in thicker and coarser deposits, suggests that the graptolites lived mainly at some distance from the shore where sediment was deposited slowly in tranquil water; and the carbonaceous matter in those shales may have been derived from the decomposition of sea-weeds.

The genera of graptolites at present accepted are based, to a large extent, on the number of branches of the polypary; but Nicholson and Marr consider that this feature is of less importance than was formerly supposed, and that a classification which shows the genealogical relationships of the forms should be founded chiefly on the characters of the hydrothecæ and, to some extent, on the angle of divergence of the branches. The early graptolites, such as *Bryograptus*, appear, at first sight, to be more advanced than the later types (*e.g.* *Monograptus*), on account of their more complex branching; but in the early forms the hydrothecæ are very simple, differing but little from the sicula, whereas in the later ones they exhibit considerable modification. In some genera the hydrothecæ of different species show great variety of form, those of one species being often much more like those of a species belonging to another genus than to other species of the same genus: thus we get the same type of hydrotheca in the three forms *Bryograptus callavei*, *Tetragraptus hicksi*, and *Didymograptus affinis*, and another type in *Bryograptus retroflexus*, *Tetragraptus denticulatus*, and *Didymograptus fasciculatus*. It is contended that each of these groups is a genealogical series and should be regarded as a genus—that *T. hicksi* has descended from

B. callavei, and *D. affinis* from *T. hicksi*. According to the old view all the species of *Didymograptus* were thought to have descended from one common ancestor; but this will not account for the close resemblance which the hydrothecæ of certain species of *Didymograptus* bear to those of certain species of *Tetragraptus*; on the other hand, this is readily explained if we consider that the species of *Didymograptus* have descended from various species of *Tetragraptus*. Then again, the remarkable diversity in the hydrothecæ of *Monograptus* can be easily understood if we grant that the forms included under this term are the descendants of different species of one or more genera. But since species which have a different ancestry cannot be placed in the same genus, we must regard *Monograptus* as an assemblage of forms which agree merely in consisting of a single uniserial branch or stipe, and have descended, through *Dimorphograptus*, from various groups of *Diplograptus* and perhaps of *Climacograptus*.

* **Didymograptus** (fig. 20). Polypary bilaterally symmetrical, consisting of two uniserial stipes diverging at an angle which varies, in different species, from 0° to 180° (or occasionally more). Hydrothecæ subcylindrical, in contact for a considerable part of their length. Lower Arenig to Upper Llandeilo. Ex. *D. murchisoni*, Lower Llandeilo; *D. patulus*, Arenig.

* **Phyllograptus** (fig. 24). Polypary leaf-like, consisting of four uniserial stipes united along the whole of their length. Hydrothecæ cylindrical or subcylindrical, in contact throughout their entire length. Sicula pointing distally. Arenig. Ex. *P. typus*.

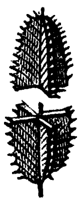


Fig. 24. *Phyllograptus*, Arenig Rocks. The polypary has been cut in two, and the upper part raised so as to show the four branches. Natural size.

* **Tetragraptus** (fig. 16). Polypary bilaterally symmetrical, uniserial, consisting of four simple ra-

diating branches which arise from the bifurcation of two short branches coming off from opposite sides of the sicula (constituting a *Didymograptus* stage). Hydrothecæ cylindrical or subcylindrical, in contact for a considerable part of their length. A central disc may or may not be present. Arenig. Ex. *T. quadribrachiatus.*

* **Dichograptus.** Polypary typically bilaterally symmetrical consisting of eight uniserial main stipes produced by bifurcation through *Didymograptus* and *Tetragraptus* stages. Hydrothecæ cylindrical or subcylindrical. A central disc is frequently present. Lower Arenig. Ex. *D. octobrachiatus.*

Loganograptus (Arenig) and *Clonograptus* (Tremadoc and Arenig) are forms in which bifurcation has proceeded further than in *Dichograptus.*

Bryograptus. Polypary bilaterally symmetrical, uniserial, consisting of two main stipes diverging at a small angle from the sicula, which has its point directed distally. From the inner margins of the main stipes similar secondary stipes (which may bear other stipes) arise. Hydrothecæ like those of *Dichograptus.* Tremadoc. Ex. *B. kjerulfi.*

Leptograptus. Polypary consisting of two simple, slender, flexuous, uniserial stipes given off in opposite directions from the sicula at angles greater than 180°. Hydrothecæ are long tubes with slight sigmoid curvature, in contact for half their length. Upper Llandeilo to Lower Bala. Ex. *L. flaccidus*, Lower Bala.

Pleurograptus. Two principal branches as in *Leptograptus*; these bear secondary branches on both sides, often arising alternately, and sometimes bearing smaller branches. Lower Bala. Ex. *P. linearis.*

Nemagraptus (=*Cœnograptus*). Polypary bilaterally symmetrical, uniserial, consisting of two slender, more or less flexuous main stipes coming off from the middle of a well-defined sicula; from each of these stipes secondary branches may be given off in a symmetrical or nearly symmetrical manner. Hydrothecæ as in *Leptograptus.* Llandeilo. Ex. *N. gracilis.*

* **Dicranograptus.** Polypary bilaterally symmetrical, biserial in the proximal portion, dividing distally into two uniserial branches.

Hydrothecæ tubular, with sigmoid curvature and inturned apertures. Upper Llandeilo to Lower Bala. Ex. *D. clingani*, Bala.

Dicellograptus. Like *Dicranograptus*, but uniserial throughout, the two branches united at the sicula only, which points distally. Angle of divergence greater than 180°. Upper Arenig to Upper Bala. Ex. *D. anceps*, Upper Bala.

Diplograptus (figs. 15 d, 19). Polypary biserial. Hydrothecæ subprismatic or subcylindrical tubes, overlapping and placed obliquely. Virgula prolonged beyond the distal extremity of the polypary. Sicula more or less completely concealed. Arenig to Tarannon. Ex. *D. foliaceus*, Llandeilo to Lower Bala. *Petalograptus* and *Cephalograptus* are sub-genera; Llandovery and Tarannon.

Climacograptus (fig. 17). Polypary biserial. Hydrothecæ tubular, with sigmoid curvature, apertures placed in depressions. Sicula often concealed. Upper Arenig to Tarannon. Ex. *C. normalis*, Llandovery and Tarannon.

Retiolites (fig. 18). Polypary biserial, straight. Hydrothecæ like those of *Diplograptus*. Periderm consists mainly of a network of threads and rods. Lower Bala to Lower Ludlow. Ex. *R. geinitzianus*, Upper Tarannon and Wenlock.

Dimorphograptus (see p. 61). Llandovery.

Monograptus (fig. 15 c). Polypary unbranched, uniserial; ~~straight, curved,~~ or spiral. Hydrothecæ vary in form in different species. Sicula attached to the proximal end of the polypary, and its pointed end directed distally. Lower Llandovery to Lower Ludlow. Ex. *M. nilssoni*, Lower Ludlow; *M. leptotheca*, Llandovery; *M. priodon*, Wenlock; *M. spinigerus*, Llandovery.

Rastrites. Closely allied to *Monograptus*, but the hydrothecæ are long, tubular, and widely separated. Llandovery to Tarannon. Ex. *R. peregrinus*, Llandovery to Tarannon.

Cyrtograptus. Similar to *Monograptus*, but coiled into a plane spiral with branches given off from the external (hydrothecal) margin. Upper Tarannon to Wenlock. Ex. *C. murchisoni*, Wenlock Shale.

Distribution of the Graptolitoidea

Cambrian. In Britain the earliest graptolites occur in the Tremadoc Beds, where we find the branching forms *Bryograptus* and *Clonograptus.*

Ordovician. The graptolites in the Arenig division are mainly uniserial forms without a virgula in the wall of the common canal and are often branched. The most characteristic genera are *Didymograptus, Tetragraptus, Dichograptus,* and *Phyllograptus*: *Clonograptus* survives from the Cambrian into the lower part of the Arenig. In the Llandeilo *Didymograptus* is still found and is fairly common in the lower part of the formation; other important genera in the Llandeilo are *Dicellograptus,* the biserial *Diplograptus* and *Climacograptus,* and *Nemagraptus* and *Dicranograptus* which now appear for the first time. In the Bala Beds, the biserial genera *Diplograptus, Climacograptus* and *Dicranograptus* become much more abundant, and with them occur *Leptograptus* and *Pleurograptus.*

Silurian. The only genera which pass up from the Ordovician to the Silurian are *Climacograptus, Diplograptus,* and *Retiolites,* and nearly all the species in the two systems are different, so that between the Ordovician and Silurian there is a great break in the graptolitic succession. As a whole, the Silurian formations are characterised by the uniserial genera *Monograptus, Rastrites* and *Cyrtograptus,* which appear first in the Lower Silurian. In the lower part of the Llandovery the genera *Diplograptus* and *Climacograptus* are fairly abundant, but they become extinct in the Tarannon, and in the Wenlock and Ludlow Beds the only forms are *Monograptus, Cyrtograptus,* and *Retiolites.* The last traces of graptolites occur in the Downtonian Beds, but they are too imperfect for determination.

ORDER IV. HYDROCORALLINA

The skeleton in the Hydrocorallina is calcareous and has the form of encrusting or branching masses. It consists of a network of rods, in which there are tubes of two sizes opening on the surface; the larger are called *gastropores*, and have horizontal partitions or tabulæ; the smaller are named *dactylopores*. The skeleton is of ectodermal origin, and is secreted by a network of cœnosarcal tubes, above which is a superficial layer of ectoderm. The polyps project above this layer, and are of two kinds: nutritive individuals or gastrozooids, which are placed in the gastropores, and dactylozooids placed in the dactylopores. The soft parts in the branching forms may extend throughout the skeleton, but in the massive forms they are limited to the superficial layers.

Millepora is an important rock-building organism at the present day, often contributing largely to the formation of coral-reefs; it has been recorded from Cainozoic deposits, but whether these examples really belong to that genus appears to be somewhat doubtful. *Stylaster* is a living form, and is stated to occur in the Miocene. *Milleporidium* from the Upper Jurassic of Stramberg and *Millestroma* from the Upper Cretaceous of Egypt may belong to this Order.

ORDER V. STROMATOPOROIDEA

In the Stromatoporoids the skeleton is calcareous, and very variable in form; it may be hemispherical, spheroidal, dendroid, encrusting, or altogether irregular, and frequently forms large masses. It consists of a series of concentric laminæ separated by spaces; these are crossed at right angles by rods or pillars, which give off horizontal processes at definite intervals; these processes join together and

really form the laminæ which are perforated by openings of various sizes. The pillars may pass only from one lamina to the next, or may be continued through a considerable number of laminæ. The under surface of the skeleton is often covered by a thin imperforate layer, with concentric furrows, similar to the epitheca of many compound corals. On the upper surfaces of the laminæ there are, in many

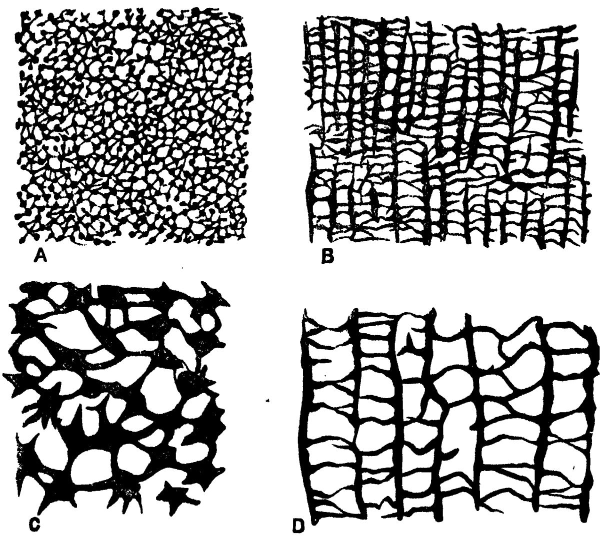


Fig. 25. A, tangential section of *Actinostroma intertextum* showing the radial pillars. B, vertical section showing the radial pillars and the formation of the concentric laminæ by processes given off from these. × 12. C and D, parts of A and B further enlarged. From the Silurian Rocks. (After Nicholson.)

forms, shallow grooves, having a stellate arrangement, and known as *astrorhizæ*; somewhat similar grooves are found on the surface of *Hydractinia*. In some genera, as for example *Actinostroma* (fig. 25), the two elements of the skeleton, the laminæ and pillars, remain quite distinct, but

in others, like *Stromatopora*, they become to a great extent blended together so as to form a more or less netted structure; between these two types, however, there are intermediate forms. The first type (*Actinostroma*) has been compared with *Hydractinia* (see p. 54), but is always calcareous and forms larger masses; the second (*Stromatopora*) shows some resemblance to *Millepora* (see p. 74), and, like that genus, possesses vertical tubes with horizontal partitions (or "tabulæ"), but the tubes seem to be of one size only, and consequently there is nothing to indicate that this type was dimorphic; it differs also in possessing radial pillars.

The soft parts in the Stromatoporoids formed a continuous layer on the surface of the skeleton, and it is believed by some authors that the polyps in some cases (*e.g. Stromatopora*) were placed in definite tubes, but in others tubes are absent and there are pores only in the external lamina. From the structure of the skeleton, it has been inferred by some palæontologists that the Stromatoporoids are connected with both *Hydractinia* and the Hydrocorallina; but this view, and even their relationship to any Hydrozoa, has been denied by others.

The Stromatoporoids are found mainly in the Ordovician, Silurian, and Devonian Systems, being most abundant in the last; frequently they are of considerable importance as rock-builders; some of the best known genera are *Labechia, Stromatopora, Stromatoporella, Actinostroma, Clathrodictyon, Idiostroma,* and *Amphipora*. A few specimens, which are believed to be Stromatoporoids, have been found in deposits of Mesozoic age.

CLASS II. SCYPHOZOA

The Scyphozoa (Scyphomedusæ) or Acalephæ include the larger and more conspicuous jelly-fishes, such as *Aurelia*, *Rhizostoma*, and *Pelagia*. They possess no hard parts; nevertheless the impressions of some forms (*e.g.* *Rhizostomites*) belonging to the Order Discomedusæ have been found in the Lithographic Limestone (Upper Jurassic) of Solenhofen in Bavaria.

Even in the oldest fossiliferous formations traces of supposed Scyphozoa have been found; the most satisfactory of these is the form from the Lower Cambrian of Sweden referred to the Discomedusæ, and named *Medusina costata* (= *Medusites lindstrœmi*). Others, but of which the nature appears to be somewhat doubtful, have been described by Walcott from the Middle Cambrian of Alabama and British Columbia.

CLASS III. ANTHOZOA (ACTINOZOA)

This Class includes the corals and sea-anemones. They differ from the Hydrozoa (1) in possessing an œsophageal tube or *stomodæum*, which is distinct from the cœlenteron, though opening into it; (2) in having the cœlenteron divided up into chambers by vertical radiating partitions known as mesenteries; (3) in the reproductive elements being developed in the endoderm of the mesenteries and never on a medusa.

The Anthozoa possess an apparent radial symmetry, but closer examination reveals a bilateral arrangement of their parts. In a typical form, such as the common sea-anemone or a simple coral (fig. 26), the body has a more or less cylindrical shape, and is attached by one end, the other having an opening, the mouth (fig. 26, 2), surrounded

by tentacles (1) The mouth leads into the *stomodæum* (3), which opens at its lower end into the cœlenteron The latter is divided into chambers by radiating partitions, the *mesenteries* (fig 26, 4 and fig 27 *a*—*c*), each of which consists of a thin gelatinous layer in the middle and a layer of endoderm on each side In the upper part of the polyp the inner edges of the principal mesenteries join the stomodæum, but in the lower part they remain free, and a

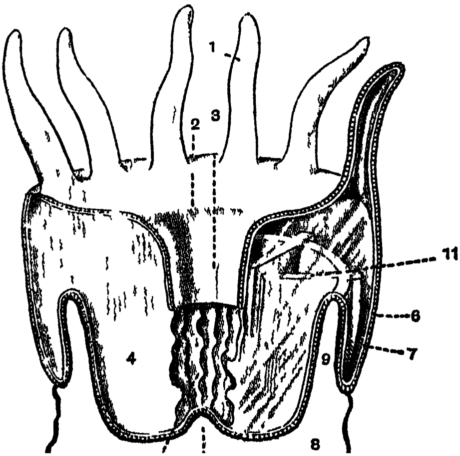


Fig 26 Semi diagrammatic view of half a simple Coral (Partly after Bourne) On the right side the tissues are represented as transparent to show the arrangement of the theca and septa, on the left a mesentery is seen 1, tentacle, 2, mouth, 3, stomodæum 4, mesentery 5, mesenteric filaments, free edge of mesentery, 6, ectoderm, 7, endoderm, 8, basal plate of skeleton, 9, theca, 10, columella, 11, septum

section in the former region (fig 27) will show the body wall and also the stomodæum, but in the latter the body wall only The tentacles (fig 26, 1) are placed immediately above the intermesenteric chambers, and the space in each

tentacle is continuous with that of the chamber below. A bilateral symmetry is indicated by the oval or slit-like mouth, and the similarly compressed stomodæum; also by the arrangement of the longitudinal muscles which occur on one face of each mesentery, extending from the base of the polyp upwards (fig. 27). The sea-anemones have no hard parts, but the majority of Anthozoa possess a skeleton, which in many cases is quite external to the body, and is formed of carbonate of lime (fig. 26, 8, 9); in others it is internal and may consist of calcareous spicules, or of an axial rod of horny or calcareous material. The Anthozoa are divided into two Orders, (1) the Zoantharia, (2) the Alcyonaria.

ORDER I. ZOANTHARIA

In the Zoantharia the tentacles are generally numerous and are never eight in number, as is the case in the Alcyonaria; occasionally there are six only, but frequently a multiple of six, and they usually form several circles around the mouth. The tentacles are nearly always simple (fig. 26, 1). The mesenteries (fig. 27, *a*, *b*, *c*) are usually numerous also and form several cycles; those belonging to the primary cycle are formed first and reach to the stomodæum; the other cycles (secondary, tertiary, etc.) are successively smaller. The mesenteries are arranged in couples (fig. 27) with the longitudinal muscles of each couple facing one another, except in the case of the couples situated at the grooved ends of the stomodæum, where the muscles are turned away from each other (*d*, *e*). Commonly there are six couples of primary mesenteries, six of secondary, twelve of tertiary, and so on. The narrow space between the two mesenteries of a couple is known as an *entocœle*; the wider space between two mesenteries of adjacent couples is known

as an *exocœle.* A skeleton is often present in the Zoantharia and may be calcareous or horny; when calcareous it is never composed of spicules but consists of aragonite fibres.

The Zoantharia comprise, (1) the sea-anemones, which have usually been grouped together as the Actinaria, and are unknown in the fossil state, since they possess no hard parts; (2) the Antipatharia—colonial forms in which the skeleton consists of an internal horny rod secreted by the ectoderm; these also are not found fossil; (3) the Madreporaria, including the well-known stony corals, which are very abundant as fossils.

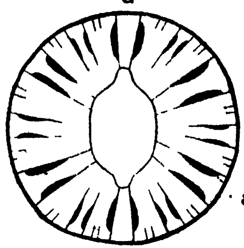


Fig. 27. Diagrammatic section of a Zoantharian polyp passing through the stomodæum. *a*, primary mesenteries; *b*, secondary mesenteries; *c*, tertiary mesenteries; *d*, *e*, primary mesenteries at the ends of the compressed stomodæum. The muscles are indicated by the thickenings on the mesenteries.

MADREPORARIA

The polyp of a Madreporarian coral has essentially the same structure as a common sea-anemone, but the ectoderm of the lower part of the body secretes a skeleton consisting of carbonate of lime (fig. 26, 8, 9). The entire skeleton is spoken of as the *corallum*, and in compound corals the skeleton of each individual is termed a *corallite.*

The parts of the skeleton may be solid, or they may be perforated, or formed of a network of rods.

In a typical simple coral (fig. 29) the skeleton has a more or less conical form; the base of the cone, on which the polyp is placed, is usually depressed, and is termed the *calyx*. The wall bounding the corallum is known as the *theca* (fig. 26, 9; fig. 28, *d*); sometimes there is, outside this, another calcareous layer, the *epitheca*. The whole space enclosed by the theca is termed the *visceral chamber*; it is divided up by various partitions, the most important of which are the *septa* (fig. 26, 11; fig. 28, *b*). These are vertical plates extending from the theca towards the centre, and alternating in position with the mesenteries. The septa are of different sizes, some reaching the centre, others being shorter; they frequently occur in series or cycles, of which three or more may often be distinguished, the largest being the *primary* (*b*), the others the *secondary*, *tertiary*, etc. Each cycle of septa agrees in position with the corresponding cycle of mesenteries, *e.g.* the primary septa are within the entocœles of the first cycle of mesenteries. In many corals found in the Palæozoic formations one of the primary septa (the cardinal septum) is much smaller than those formed after it, and consequently appears, at the surface of the calyx, to lie in a pit or cavity, which is called a *fossula* (figs. 38 *a*, 39 A, *a*). Usually only one fossula is present—the *cardinal fossula*, but sometimes others, known as the *counter* and *alar fossulæ* are found (fig. 39 A, *dd*, *e*) (see p. 89).

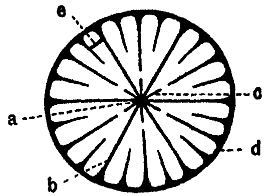


Fig. 28. Diagrammatic section (horizontal) of a simple coral. *a*, columella; *b*, primary septa; *c*, pali; *d*, theca; *e*, dissepiments.

When the septa project upwards above the edge of the theca they are said to be *exsert* (fig. 29). The faces of the septa are sometimes plane, but usually bear ridges, granules, or spines. In some corals the septa are poorly developed, and may be represented by ridges only or by rows of spines. In the centre of the coral, where the larger septa meet, there is often a vertical rod, which extends from the base of the chamber to the bottom of the calyx; this is the *columella* (figs. 28 *a*; 36 *c*). Its structure varies considerably; when it is solid and ends in a knob or point in the calyx, it is said to be *styliform*; sometimes the top is porous or *spongy*. When the columella consists of twisted laminæ it is termed *trabeculate*; if formed by the twisting together of processes given off from the inner edges of the septa, it is *false*: in some genera there is no columella. Other vertical partitions, somewhat similar to the septa, are the *pali* (fig. 28 *c*); these are radiating plates attached to the columella and placed opposite the inner edges of some of the shorter septa, but not joining them. Bars or rods, known as *synapticulæ*, are often found joining one septum to another. Similarly, adjacent septa are often connected by thin plates, which may be horizontal or oblique, straight or curved, and are called *dissepiments* (figs. 28 *e*; 36 *d*); in some genera they are very abundant near the margin of the visceral chamber and form a spongy or *vesicular* tissue (fig. 34 *d*). *Tabulæ* are more or less horizontal plates which cross the septa, and occupy the central part of the visceral chamber, or, when well developed, extend quite across it (figs. 34 *t*;

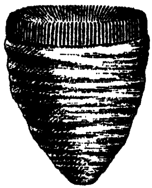


Fig. 29. *Montlivaltia trochoides*, Inferior Oolite, showing exsert septa. × ½.

36 B, *t*); they are arranged one above another, so that the visceral chamber is divided into horizontal compartments. On the outside of the wall of the coral there are, in some forms, vertical ridges, which may be smooth or spiny; these are known as *costæ*, and usually correspond in position with the septa.

In one family of Rugose Corals found in the Carboniferous there is a large cylindrical column in the centre of the coral which projects up into the calyx; it may be formed of vertical radiating plates crossed by transverse plates or of irregular plates forming a vesicular tissue (figs. 37, 38).

The young coral polyp is a free-swimming animal; when it becomes fixed the first part of the skeleton to appear is a circular plate between the base of the polyp and the surface to which it is attached; on this basal plate radial ridges—the first traces of the septa—are secreted in folds formed in the base of the polyp between each couple of primary mesenteries. The theca next appears at the edge of the septa, and is formed either by the union of the thickened ends of the septa, or as an independent secretion between the ends of the septa. At the edge of the basal plate an upgrowth may occur forming the epitheca outside the theca. For some time the polyp extends down to the base of the cup-like skeleton (fig. 26) and a fold hangs over the outside (fig. 26, 6, 7); but as the septa and theca increase in height the lower part of the visceral chamber becomes (in most cases) more or less completely cut off by the development of dissepiments or tabulæ which are secreted by the basal part of the polyp, and below which the soft parts do not extend. As growth proceeds more of these partitions are formed, and eventually a large part of the coral ceases to have any direct connexion

with the polyp. On account of the septa and columella the basal wall of a coral polyp, unlike that of a sea-anemone which remains flat, becomes greatly infolded; the infolds occur between every two mesenteries. The parts of the coral skeleton described above are entirely *external* to the polyp; but the synapticulæ, on the other hand, perforate the mesenteries and the basal wall of the polyp, and are formed by the growth and ultimate fusion of two opposite granules on the faces of adjacent septa.

Some corals remain simple (*i.e.* consist of a single individual) throughout life. Others, which are simple in

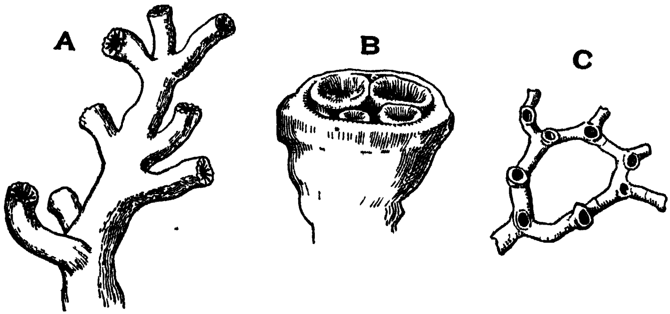


Fig. 30. A. *Dendrophyllia nigrescens*, showing corallites which have been produced by lateral budding. Recent. ×½. B. *Cyathophyllum truncatum*, showing calicular budding, Wenlock Limestone. Natural size. C. *Cladochonus crassus* (seen from above), showing basal budding, Carboniferous Limestone. Natural size.

the young state, afterwards become compound and form colonies, either by giving off buds, or by fission. In budding, new individuals may arise from the part of the polyp which extends outside the theca (fig. 26, 6, 7), in which case a branching coral like *Dendrophyllia* (fig. 30 A) is frequently formed; this mode of increase is termed *lateral budding*. In other cases buds arise on the upper surface of the old polyp, and then the young corallites are found inside the calyx of the parent—hence this is known

as *calicular* budding (fig. 30 B). In *basal budding* (fig. 30 C), which is rare in the Madreporaria but common in the Alcyonaria, the buds spring from creeping prolongations or stolons, which are given off from the base of the coral. Fission, or division into halves, commences by the mouth becoming slightly constricted in the middle; this increases gradually until two distinct mouths and two polyps are formed, after which a similar division takes place in the skeleton. When the individual corallites in a compound coral are free and diverge from one another,

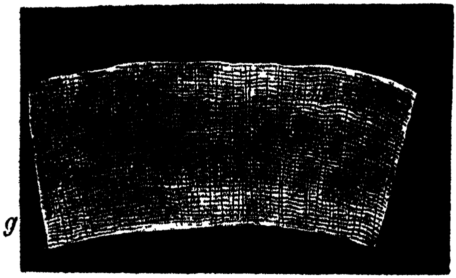


Fig. 31. Section of a dissepiment of *Galaxea*. Magnified. *g*, growth-lamellæ. (From M. M Ogilvie.)

the corallum is termed *dendroid* (fig. 30 A): when they are in contact, it is *massive*. If the corallites are not in contact the spaces between the individual corallites are sometimes filled up with calcareous material formed by the cœnosarc, and known as *cœnenchyma*. In massive corals (*e.g. Acervularia*) the base of the corallum is sometimes covered by a thin epithecal plate—the *basal epitheca*.

In dendroid corals the polyps on the different corallites may be quite separate from one another; but in massive corals, whilst the upper parts of the polyps are more or less separate, the lower parts are united and the cœlentera of adjacent individuals communicate with one another.

When cœnenchyma is present the polyps are united by an extension of the part which ordinarily occurs outside the theca, and now forms a sheet called the cœnosarc.

Microscopic examination of thin sections shows that each part of a coral is formed of thin layers or growth-lamellæ which consist of fine needle-like crystals placed more or less perpendicularly to the surfaces of the lamellæ.

Fig. 32. Transverse section of part of a septum and theca of *Galaxea*. Highly magnified. *d*, dark spots; *g*, growth-lamellæ; *a*, granule on septum. (From M. M. Ogilvie.)

In a dissepiment the upper surface only is covered by the soft parts, and a section shows (fig. 31) a series of lines parallel to the surface and other finer lines crossing at right angles are seen—the former mark the growth-lamellæ, the latter the crystalline fibres. In a septum both sides are covered by the soft parts, and a transverse section shows (fig. 32) a median dark line or row of dark spots, on each side of which the structure is symmetrical. When

the surface of the septum is plane, the lamellæ are straight, or nearly straight, and parallel with the surface, and the fibres are perpendicular; but when the surface is ridged the lamellæ are curved so as to be parallel with the ridges, and the fibres radiate out from the dark median spots toward the curved surface of the ridge (fig. 32). When the septa bear striæ, granules, or spines, in addition to ridges, the folding of the lamellæ and the radiating arrangement of the fibres become more complex; but in all cases the structure is directly related to the form of the surface. The dark lines and spots represent the part of the septum which was first secreted; their dark appearance may be due either to the less regular arrangement of the fibres or to the imperfect calcification of the material of that part. In fossil corals the dark part has often undergone secondary changes which give it a more distinct appearance.

In the development of a living Zoantharian coral six primary septa are first formed and appear simultaneously[1], one septum between each couple of primary mesenteries; next, six secondary septa are introduced between the primary septa, either simultaneously or in bilateral pairs from the dorsal to the ventral border; other cycles may subsequently be added in a somewhat similar manner, not simultaneously, but in successive bilateral pairs; in the adult all the septa have generally a completely radial arrangement. In the Rugose corals of the Palæozoic period the development[2] of the septa follows a different course.

[1] In some corals twelve septa are first developed simultaneously, of which six grow more rapidly than the others and become the primary septa.

[2] This can be studied by gradually grinding down the tip of a perfect specimen. The arrangement of the septa in Rugose corals can also be seen either on the surface of the wall or by removing the theca.

Instead of the six primary septa appearing simultaneously, two septa (fig. 33 A), one on each side, are first formed and meet in the centre of the coral—representing the cardinal (1) and counter septa (1′) of the adult, on the ventral and dorsal sides respectively (fig. 39 A, *a*, *b*); next, two more septa (fig. 33 B, 2) appear, one on each side of the cardinal

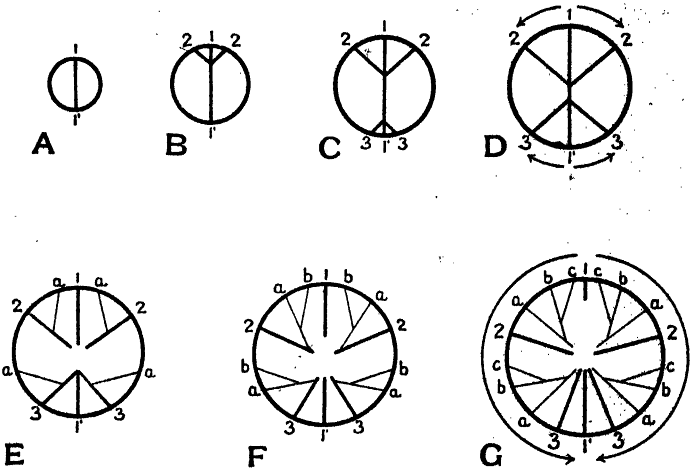


Fig. 33. Development of the septa in a simple Rugose Coral, *Zaphrentis*. 1—3, primary septa; 1, cardinal septum; 1′, counter septum; 2, alar septa; 3, counter-lateral septa; *a*, *b*, *c*, later septa (metasepta). (After Carruthers.)

septum, and as growth proceeds these become more widely separated from the cardinal septum, and eventually form the alar septa of the adult (fig. 39 *c*); afterwards, two septa (3) are added, one on each side of the counter septum, and these also spread outwards as growth proceeds (as indicated by the arrows in fig. 33 D). The six septa now present are regarded as the primary septa (1, 2, 3). The later septa (sometimes termed *metasepta*) are introduced in pairs; these appear at four points—one septum on each side of the

cardinal septum (1), and one between each alar septum (2) and the primary septum (3). The two pairs which are first added (fig. 33 E, *a*) are attached to the cardinal sides of the primary septa 2 and 3; similarly later pairs (fig. 33 F, G, *b*, *c*) are introduced and are joined to the cardinal sides of the previously formed septa. As growth proceeds all the later septa (*a*—*c*), unlike the primary septa, gradually move towards the counter septum, as indicated by the arrows in fig. 33 G.

In the adults of some Rugose corals (fig. 39 A) the arrangement of the septa is similar to that just described, so that on each side of the cardinal fossula and on the counter side of each alar septum the later septa (metasepta) have a pinnate arrangement. In other genera, however, the pinnate plan is not seen in the adult (figs. 37, 38), since in the later stages of growth all the septa either become free at their inner edges or unite only at the centre of the coral; and in such cases, unless a fossula is present, the symmetry of the coral is nearly or quite radial.

From the description of the septal development given above, it will be seen that the fossulæ are breaks in the sequence of the septa. The cardinal fossula (fig. 39 A, *a*) is limited by the later septa added on each side of the small cardinal septum. The counter fossula, on the opposite side, where no new septa are introduced, is bounded by the two primary septa (*d*, *d*) which enclose the counter septum (*b*). The alar fossulæ are the spaces between each alar septum (*c*) and the newer septa which have been added on its counter side.

The fossulæ have been regarded as pits or chambers for those mesenteries which alone were specialised for reproduction. Another explanation of the nature of the cardinal fossula is that it is due to the presence of a groove on the

ventral side only of the stomodæum, similar to that found in the living family Zoanthidæ; it is thought that such a groove would account for the small size of the cardinal septum.

By many authors the Madreporarian corals have been divided into three sections: (1) the Aporosa, (2) the Perforata, and (3) the Rugosa. The characters of these groups are:—

(1) *Aporosa.* Theca and septa solid, the latter radially arranged, with usually six primary septa. Tabulæ usually not clearly differentiated. Fission common.

(2) *Perforata.* Distinguished from the Aporosa by the septa and theca being perforate. Where the perforations are numerous the skeleton is light and porous and appears to consist of a network of rods. In living corals the perforations are traversed by canals of the soft parts.

(3) *Rugosa.* Septa and theca solid; tabulæ and dissepiments usually well developed and clearly differentiated. The coral is usually bilaterally symmetrical owing to the pinnate arrangement of the septa and to the presence of one or more fossulæ (fig. 39). New septa are introduced along four lines only. In the adult coral the septa are usually of two sizes, alternately long and short. Increase takes place by budding, *not* by fission. The Rugosa are almost limited to the Palæozoic formations; the name of the group is taken from the vertical ridges often seen on the wall of the coral.

The separation of the Aporosa from the Perforata cannot be maintained since it has been shown that corals with a perforate skeleton have arisen independently from more than one group of Aporose corals.

Until recently it has been generally maintained that

the Rugosa possess only four primary septa—the cardinal, the counter, and two alar septa, which divide the coral into quadrants; on account of this the name Tetracoralla has sometimes been used for this group. The study of the development of the septa has shown that there are really six primary septa, and the Rugose corals consequently agree in that respect with Aporose corals, so that it is possible that both may have descended from the same ancestors; the difference in the mode of development of the later septa, however, seems to indicate that the two groups soon diverged. A difficulty in accepting this view of their common ancestry is due to the fact that Rugose corals are found as early as the Ordovician, whereas Aporose corals are not known to occur in the Palæozoic formations. It is also possible that Aporose corals may have descended from a Palæozoic Anthozoan which possessed no skeleton.

Another view is that the Rugose corals do not form a natural group, since the bilateral symmetry, the fossulæ, etc., which were regarded as characteristics, are not in all cases found in adult specimens; on the other hand, some of the Mesozoic genera of Aporose corals are stated to possess fossulæ and a bilateral symmetry, and to show in the young stages a pinnate arrangement of septa like that found in Rugose corals. Also some of the families of Aporose corals, particularly those found in the Trias and Jurassic, are said to possess features similar to those of certain Rugose families of the Palæozoic period, from which it is inferred that they are the descendants of the latter. Thus, for example, the Astræidæ (Aporosa) are believed by some authors to be closely related to the Cyathophyllidæ (Rugosa), and the Turbinolidæ (Aporosa) to the Zaphrentidæ (Rugosa). If this view of the relationship of Aporose and Rugose families is correct, it is obvious

that the Rugosa and Aporosa cannot be regarded as natural groups, of which the former became extinct or nearly extinct at the close of the Palæozoic period, but that different Rugose families are the ancestors from which a number of Aporose families have sprung independently.

Until more is known of the phylogeny of corals it will be convenient to divide the genera described into two groups (1) Rugose, (2) Aporose and Perforate.

1. *Rugose Corals.*

* **Cyathophyllum** (fig. 34). Simple or compound: often massive. Septa numerous, of two sizes, alternating, the longer reaching the centre where they may give rise to a false columella. Fossula often absent. Tabulæ rather small, occupying the central part only of the visceral chamber. Dissepiments form an extensive peripheral zone of vesicular tissue. Bala to Carboniferous. Ex. *C. murchisoni*, *C. regium*, Carboniferous Limestone.

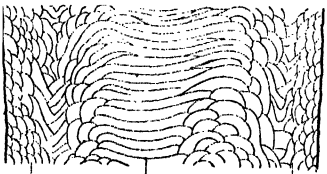


Fig. 34.

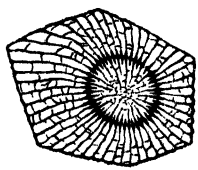


Fig. 35.

Fig. 34. *Cyathophyllum murchisoni*, Carboniferous Limestone. Portion of a vertical section. *d*, dissepiments; *t*, tabulæ.

Fig. 35. *Acervularia luxurians*, Wenlock Limestone. Horizontal section of one corallite. × 1½.

Acervularia (fig. 35). Compound, massive; corallites with an outer polygonal (frequently hexagonal) theca, and an inner circular wall formed by the thickening of the septa. Septa well developed, the longer reaching the centre. Columella absent. Tabulæ extend across the central part of the visceral chamber. Dissepiments form a peripheral zone of vesicular tissue. Silurian to Devonian. Ex. *A. ananas*, Silurian. In the Devonian species the theca tends to become reduced, thus approaching *Phillipsastræa*.

Phillipsastræa (=*Smithia*). Compound, massive. Septa numerous, becoming thickened between the margin and centre of the corallite; only the longer septa extend inside this thickening towards the centre of the corallite. Septa of adjacent corallites often confluent. (The ridges sometimes seen on the sides of the septa are due to the imperfectly preserved remains of dissepiments.) Theca thin or absent. No columella. Tabulæ and dissepiments well developed, the former concave. Devonian. Ex. *P. hennahi* and *P. pengellyi*.

* **Lithostrotion** (fig. 36). Compound, either massive and with prismatic corallites, or formed of separated, nearly parallel, cylindrical corallites. Septa well developed, alternately long and

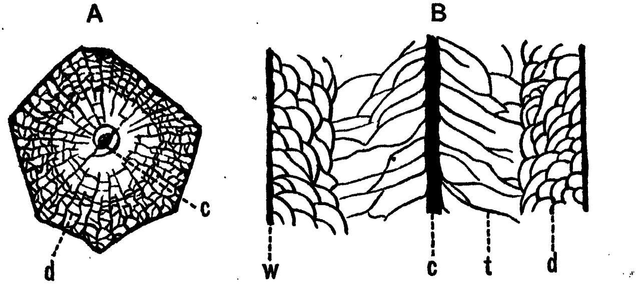


Fig. 36. *Lithostrotion basaltiforme*, Carboniferous Limestone. A. Horizontal section of a single corallite, ×2½. B. Vertical section, ×5. *c*, columella; *t*, tabulæ; *d*, dissepiments; *w*, theca.

short. Columella rod-like, laterally compressed. Peripheral zone of dissepiments narrow. Tabulæ wide, occupying the centre of the visceral chamber. Fossula often distinct. Carboniferous. Ex. *L. basaltiforme*.

* **Omphyma.** Simple, turbinate or conical. Septa numerous, alternately long and short, but extending only a short distance into the visceral chamber, the central part being occupied by tabulæ. Four shallow fossulæ are present. No columella. Peripheral zone of dissepiments relatively narrow. The theca gives off root-like processes. Bala to Lower Ludlow. Ex. *O. subturbinata*, Wenlock Limestone.

Clisiophyllum (fig. 37). Simple, turbinate or subcylindrical. Septa numerous, alternately long and short; a well-marked cardinal fossula. The large central column consists of vertical radiating

plates crossed obliquely by inclined plates, and forms a prominent projection at the bottom of the calyx. The column is surrounded by a zone formed of tabulæ, and external to this is a large zone of dissepiments. Carboniferous. Ex. *C. bipartitum.*

Dibunophyllum. Like *Clisiophyllum* but with a strong median vertical plate across the central column. Carboniferous. Ex. *D. muirheadi.*

Aulophyllum (=*Cyclophyllum*) (fig. 38). Similar to *Clisiophyllum* but with the central column surrounded by a distinct wall which is produced on one side into an angular or ridge-like projection pointing towards the fossula; central column vesicular formed of irregular plates. Carboniferous. Ex. *A. fungites.*

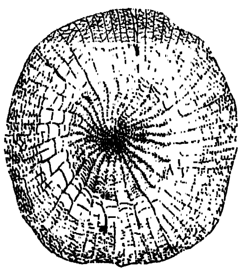


Fig. 37.

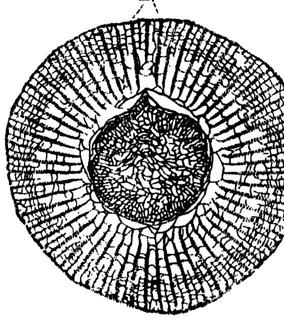


Fig. 38.

Fig. 37. *Clisiophyllum bipartitum*, Carboniferous Limestone. Horizontal section showing the large central column. Natural size.

Fig. 38. *Aulophyllum* [*Cyclophyllum*] *fungites*, Carboniferous Limestone. Horizontal section. *a*, cardinal fossula. × 1½.

* **Lonsdaleia.** Compound, either massive with polygonal corallites, or fasciculate with cylindrical corallites. Septa do not reach the theca, the marginal part of the corallite being formed of dissepiments only. Tabulæ more or less nearly horizontal, widely spaced; central column similar to that of *Dibunophyllum.* Carboniferous. Ex. *L. duplicata.*

Cyathaxonia. Simple, turbinate or elongate-conical. Septa reach the columella, which is solid. Fossula present. Tabulæ sometimes present. No dissepiments. Carboniferous. Ex. *C. cornu.*

* **Zaphrentis** (fig 39). Simple, free, bilateral; turbinate, conical, or cylindrical, often curved; calyx deep; theca thick. A well-marked cardinal fossula is present. Septa moderately numerous, the larger reaching very nearly or quite to the centre, the smaller usually short. Tabulæ well developed, extending quite across the visceral chamber. No true dissepiments. Columella absent. Silurian to Carboniferous. Ex. *Z. delanouei*, Carboniferous Limestone.

Amplexus. Similar to *Zaphrentis*, but generally cylindrical, and with very short septa. Devonian and Carboniferous. Ex. *A. coralloides*, Carboniferous.

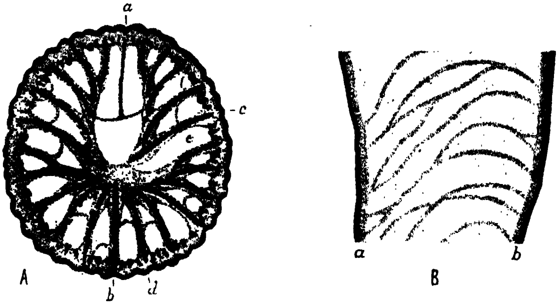


Fig. 39. *Zaphrentis delanouei*, Carboniferous Limestone. A. Horizontal section; *a*, cardinal septum in fossula; *b*, counter septum; *c*, alar septa; *d*, counter-lateral septa bounding the counter fossula; *e*, alar fossula. B. Vertical section showing tabulæ bending down into the cardinal fossula (*a*); (*b*), counter side. ×5. (Drawn by R. G. Carruthers.)

Caninia. Form similar to *Zaphrentis* but often cylindrical and slender. The longer septa meet in the centre of the lower part of the coral, but are usually short in the upper part. No columella. Tabulæ well developed. A peripheral ring of more or less vertical dissepiments is present in the adult part. Carboniferous. Ex. *C. cornucopiæ*.

Streptelasma. Simple, conical or turbinate, bilateral, with a thick wall. Septa numerous, alternately long and short. A fossula usually present, but sometimes indistinct or wanting. Columella large, false, trabeculate. Tabulæ irregular, usually poorly developed. Dissepiments moderately developed. Ordovician and Silurian. Ex. *S. corniculum*, Ordovician.

Cystiphyllum (fig. 40). Nearly always simple, conical. Septa and tabulæ absent or rudimentary; visceral chamber filled with vesicular tissue, the outer part consisting of dissepiments, the central part representing tabulæ. Fossula sometimes present. Columella absent. Calyx often deep, commonly with ridges representing septa. Silurian and Devonian. Ex. *C. vesiculosum*, Devonian.

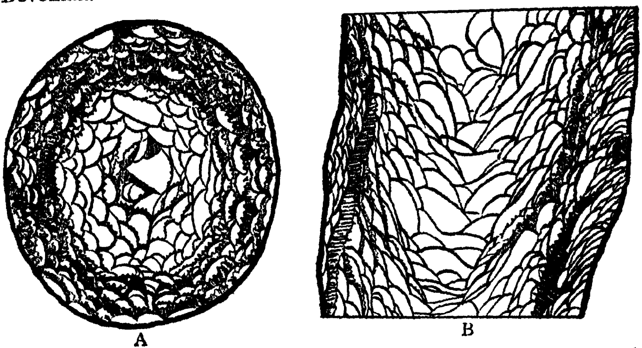


Fig. 40. *Cystiphyllum cylindricum*, Wenlock Limestone. A, horizontal; B, vertical section. (From Nicholson.) × 2.

Calceola (fig. 41). Simple, conical or slipper-shaped, one side is flat, the other convex; calyx very deep and closed by a semilunar

Fig. 41. *Calceola sandalina*, from the Middle Devonian. A, showing interior of calyx; B, inside of operculum of the same. Natural size.

operculum, which has on its inner surface a strongly-marked median ridge and several less prominent lateral ridges; septa indicated by striæ in the calyx; wall thick. Middle Devonian. Ex. *C. sandalina*.

* **Goniophyllum.** Similar to *Calceola*, but quadrangular; operculum consists of four plates forming a pyramid over calyx. Visceral chamber filled with vesicular tissue. Silurian. Ex. *G. fletcheri*, Wenlock Limestone. An operculum also occurs in the allied genus *Rhizophyllum*, Silurian.

2. *Aporose and Perforate Corals.*

Turbinolia. Simple, conical, free; calyx circular, with projecting columella. Septa exsert. Costæ lamellar, projecting, with pits in the grooves between them. No dissepiments or tabulæ. Eocene, Oligocene, and Recent. Ex. *T. humilis*, Barton Beds.

Flabellum. Simple, compressed, fan-shaped, free or fixed by rootlets. Calyx narrow, deep; septa numerous. Columella trabeculate. Costæ smooth or spiny. Upper Cretaceous to present day. Ex. *F. woodi*, Coralline Crag.

* **Montlivaltia** (fig. 29). Simple, fixed or free; turbinate, cylindrical, conical, or discoidal. Epitheca well developed, corrugated; theca thin. Columella absent. Septa numerous, strong, often exsert, the upper edges dentate. Dissepiments abundant. Trias to Recent; in England, Lias to Corallian. Ex. *M. trochoides*, Inferior and Great Oolite.

Parasmilia. Simple, fixed, turbinate or elongate. Calyx circular. Columella spongy. Septa well developed, exsert, granular on the sides. Wall with costæ. Cretaceous to present day. Ex. *P. centralis*, Chalk.

* **Isastræa.** Compound, massive; calyces polygonal. Walls of the corallites fused along their entire length. Columella rudimentary or absent. Septa thin and close together. Dissepiments abundant. Trias to Eocene; in England, Lias to Upper Greensand. Ex. *I. explanata*, Corallian.

Stylina. Compound, usually massive; calyces circular, projecting, usually separated. Columella small, styliform. Septa exsert. Dissepiments abundant. Corallites united by costæ. Basal epitheca with folds. Trias to Cretaceous; in England, Inferior Oolite to Corallian. Ex. *S. tubulifera*, Corallian.

* **Thecosmilia.** Compound, dendroid or rarely almost massive. Multiplication by fission. Margins of calyces irregular. Columella

rudimentary or absent. Septa strong, upper edges dentate, more or less exsert. Dissepiments abundant. Epitheca thick and folded, but often not preserved. Trias to Tertiary; in England, Lias to Kimeridgian. Ex. *T. annularis*, Corallian and Kimeridgian.

Holocystis. Compound, massive, convex; calyces polygonal. Columella very small or absent. Corallites united by their walls or by costæ. The four principal septa are much better developed than the others. Tabulæ well developed. Lower Greensand. Ex. *H. elegans.*

Thamnastræa. Compound, massive; convex or laminar. Walls of the corallites indistinct. Calyces shallow. Septa formed of fan-shaped rows of rods; the septa of adjoining corallites confluent; faces of septa with granulations. Columella small, trabeculate. Dissepiments present, synapticulæ numerous. Usually a basal epitheca. Trias to Miocene; in England, Lias to Upper Greensand. Ex. *T. arachnoides*, Corallian.

Micrabacia. Simple, free, discoidal, base concave. Columella false. Septa numerous, with their outer edges perpendicular. Synapticulæ present. Theca on the base only, thin; costæ granular. Upper Cretaceous. Ex. *M. coronula.*

Goniopora (=*Litharæa*). Compound, massive, perforate. Calyces more or less polygonal. Septa well developed, the faces spiny, the upper edges dentate. Walls of the corallites reticulate. Columella formed by the ends of the septa. Cretaceous to present day, common in the Eocene. Ex. *G. websteri*, Bracklesham Beds.

ORDER II. ALCYONARIA

The Alcyonaria are nearly all colonial organisms; the polyps possess eight mesenteries and eight tentacles, the latter being provided with pinnules (fig. 42, 4). In the stomodæum there is only one groove with cilia, and the longitudinal muscles (fig. 43, 6) on the mesenteries are all directed toward the groove. All the mesenteries reach the stomodæum (1). The nature of the skeleton varies considerably; in *Alcyonium* it consists of isolated spicules of carbonate of lime embedded in the common gelatinous base

from which the polyps arise. In some cases it has the form of an axial rod surrounded by the soft parts; this rod may consist of horny material (*e.g. Gorgonia*) or of carbonate of lime (*e.g. Corallium*, the red coral), or it may be formed of alternating segments of horny and of calcareous material as in *Isis*. In the 'organ-pipe coral' (*Tubipora musica*,

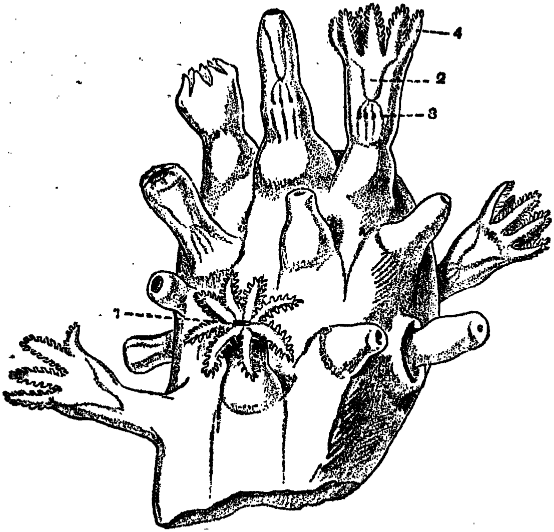


Fig. 42. Part of a colony of *Alcyonium digitatum* showing thirteen polyps in various stages of retraction and expansion. (From Shipley and MacBride.) 1, mouth; 2, stomodæum; 3, mesenteries; 4, tentacles. × 8.

fig. 44) the skeleton consists of numerous parallel tubes or corallites (*a*) which are not in contact but are held together by horizontal calcareous plates or 'platforms' (*b*). The walls of the corallites, although apparently quite compact, are really composed of spicules which have serrated edges and are firmly fitted together. A single polyp lives at the summit of each corallite; spicules occur in the middle

gelatinous layer of the polyp, and in the lower part become interlocked to form the solid wall of the corallite. The interior of each corallite is divided up by tabulæ which are often funnel-shaped (fig. 44 *c*).

In some of the Alcyonaria, as for example *Pennatula*, there are in addition to the ordinary polyps (or *autozooids*) others of a more rudimentary character, known as *siphonozooids*, in which tentacles are absent.

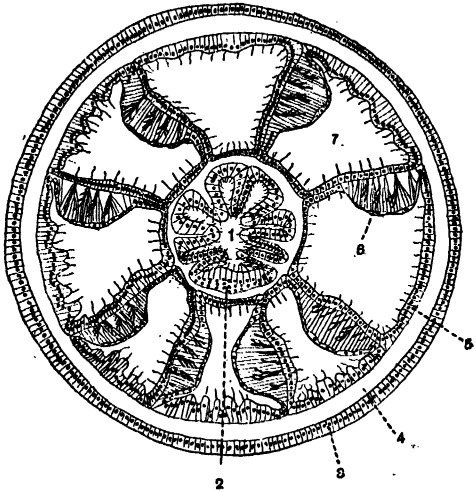


Fig. 43. Transverse section through a polyp of *Alcyonium digitatum* in the region of the stomodæum. × about 120. 1, cavity of stomodæum; 2, ventral groove with cilia (siphonoglyph); 3, ectoderm; 4, gelatinous layer; 5, endoderm; 6, muscles of mesenteries; 7, cavity between mesenteries. (After Hickson.)

The blue coral (*Heliopora*) differs from other living Alcyonaria in that the skeleton consists of calcareous fibres instead of spicules, and in this respect resembles the Madreporaria. *Heliopora* has the form of branched or lobed masses, and is composed of tubes of two sizes; the larger tubes or corallites are circular and possess usually

fifteen spine-like projections at their summits with ridges below; these are called pseudosepta, since they are not

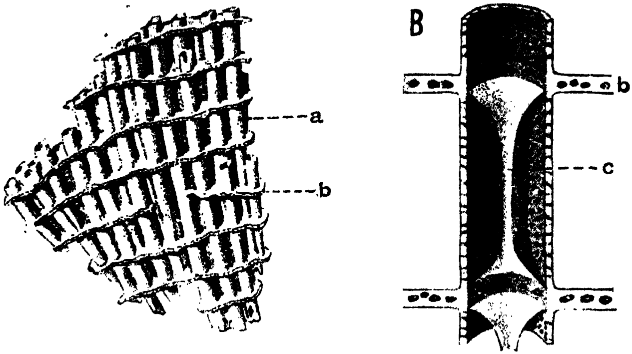


Fig. 44. *Tubipora musica*, Recent. A. Part of a colony, natural size. B. Diagrammatic vertical section of one corallite (enlarged) showing canals in the wall and platform. *a*, corallite; *b*, platform; *c*, tabula.

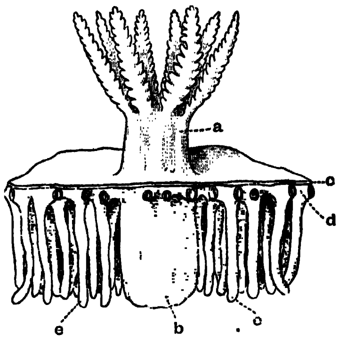


Fig. 45. *Heliopora cærulea*. A single polyp and the adjacent soft parts. *a*, the projecting part of the polyp with eight pinnate tentacles; *b*, lower part of the polyp; *c*, ectoderm; *d*, sheet of canals; *e*, cæca. (After Bourne.)

related to the number of mesenteries and do not correspond with true septa. The smaller tubes form a cœnenchyma between the corallites, and are more irregular in form.

Both corallites and cœnenchymal tubes are divided by horizontal plates or tabulæ. The soft parts form a thin sheet over the surface of the skeleton; polyps (fig. 45, *ab*) are placed in the corallites and give off branching tubes (*d*) which cover the cœnenchyma and send blind prolongations or cæca (*e*) into its tubes. The cæca were formerly regarded as siphonozooids.

Alcyonaria are rare as fossils (p. 108), unless the 'Tabulate Corals' of the Palæozoic, described below, be included in that group.

Tabulate Corals

In the Palæozoic formations numerous compound corals are found, the systematic position of which cannot yet be established; they are characterised by their numerous and well-developed tabulæ, by the septa being, in most cases, represented by ridges or spines only, and usually by the long, slender, tube-like corallites. Some of these corals present considerable resemblance to living Alcyonaria; for example, *Syringopora* is similar to *Tubipora*, and *Heliolites* to *Heliopora*: on account of this, many authors maintain that these fossil forms belong to the Alcyonaria, but this relationship is denied by other writers who point out that the skeleton is not formed of spicules, but is similar in structure to that of Zoantharian corals, and further that there is a close resemblance between *Favosites* and the living Zoantharian *Alveopora*; if it could be shown that these two forms are related, then it would follow that *Favosites* and other allied fossil genera (including *Syringopora*) must be placed in the Zoantharia. Other views of the affinities of these Palæozoic corals are (1) that they do not belong to either the Zoantharia or the Alcyonaria, but constitute an isolated group of the Anthozoa, (2) that they have been

derived from early forms of the Rugose corals, of which they form a specialised offshoot; the evidence for this view appears to be furnished chiefly by the Heliolitidæ.

A few species which appear to be allied to the Palæozoic forms have been found in deposits of Mesozoic age.

* **Syringopora** (fig. 46). Compound; corallites tubular, for the most part not in contact, more or less parallel to one another. The interiors of the different corallites communicate by means of horizontal connecting tubes. Septa feebly developed, generally represented by spines. Tabulæ numerous, more or less funnel-shaped. Budding basal. Llandovery to Carboniferous Limestone. Ex. *S. reticulata*, Carboniferous.

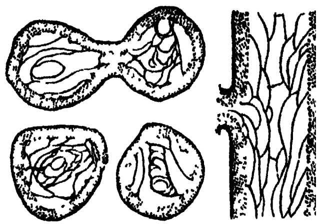


Fig. 46. *Syringopora reticulata*, Carboniferous Limestone. Horizontal and vertical sections of corallites, × 5.

Syrinogopora agrees with *Tubipora* (fig. 44) in consisting of parallel, cylindrical corallites, which have funnel-shaped tabulæ, and in its basal-budding; it differs from *Tubipora* in having much thicker walls which are not composed of spicules, and are not perforated by minute canals; also in the tabulæ being much less regular in form and position, and in possessing septa in the form of spines. The platforms of *Tubipora* (which are traversed by canals opening into the corallites) are represented by the connecting tubes of *Syringopora*; in one species of *Syringopora* (*S. tabulata*) the resemblance is particularly close, since the connecting tubes are given off from the corallites at definite levels in a radiating manner. On the other hand it must be noted that *Heterocœnia provincialis*, an Aporose coral from the Chalk, closely resembles *Tubipora* in its general build, although having no relationship to the latter. No fossil forms which would connect the Palæozoic *Syringopora* with the recent *Tubipora* have been found in Mesozoic or Tertiary formations.

Favosites (fig. 47). Compound, massive, sometimes branched. Corallites long and polygonal; the walls are in contact but not fused,

and are perforated by pores ('mural pores') arranged in rows along each face. Septa absent or represented by rows of spines. Tabulæ numerous, regular, generally extending quite across the corallite. Basal epitheca present. Bala to Carboniferous Limestone. Ex. *F. gothlandica*, Silurian.

Favosites is related to *Syringopora*, but the corallites are in contact, and consequently connecting tubes are absent, though probably represented by the mural pores. The living Madreporarian *Alveopora* agrees in general structure with *Favosites*, but its walls are less compact, and its basal epitheca is quite small. Some corals (*e.g. Koninckia, Ubaghsia*) which resemble *Favosites* are found in the Upper Cretaceous, and are regarded by some writers as links between *Favosites* and *Alveopora*. *Alveopora* has been recorded from the Upper Cretaceous of Portugal, and from the Oligocene of Styria.

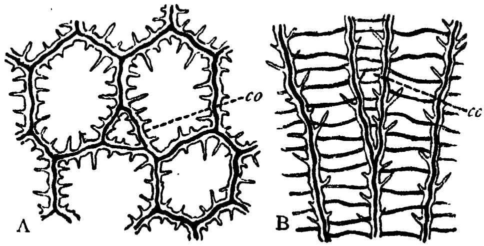


Fig. 47. *Favosites*, Silurian. A, horizontal; B, vertical section. *co*, young corallite. (From Nicholson.) ×5.

Pachypora. Similar to *Favosites*, but the walls of the corallites are greatly thickened, especially near the surface of the coral, by a secondary deposit of carbonate of lime. Silurian to Carboniferous. Ex. *P. cervicornis*, Devonian.

Alveolites. Allied to *Favosites*. Massive, encrusting, or branching. Corallites laterally compressed, with thin walls and large mural pores. Silurian and Devonian. Ex. *A. labechei*, Silurian.

Pleurodictyum. Compound, discoidal, attached by part of the base, upper surface slightly convex. Corallites diverge from the centre of the base; walls thick, with irregular pores. Septa rudimentary. Tabulæ not numerous, more or less united. A basal epitheca. Silurian and Devonian. Ex. *P. problematicum*, Devonian.

Michelinia. Similar to *Pleurodictyum*, but the tabulæ are more numerous and form a vesicular tissue, and root-like processes are usually given off from the epitheca on the base of the coral. Devonian and Carboniferous. Ex. *M. favosa*, Carboniferous.

Heliolites (fig. 48). Corallum compound, massive or branching, formed of tubes of two sizes; the larger circular ones are the corallites, between which are the smaller polygonal tubes forming the cœnenchyma. Tabulæ occur in both, and in the corallites there are septa which are usually lamellar and are generally twelve in number. Columella sometimes found in the corallites. Bala to Devonian. Ex. *H. porosus*, Devonian.

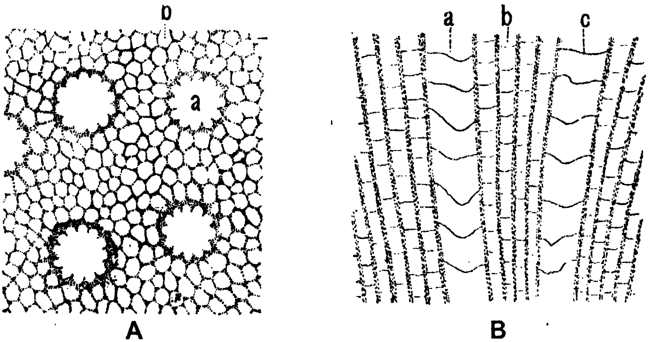


Fig. 48. *Heliolites porosus*, Devonian. A. Horizontal section. B. Vertical section. *a*, corallites; *b*, tubes forming the cœnenchyma; *c*, tabulæ. × 5.

In general structure *Heliopora* is similar to *Heliolites*, but is more branching, whilst *Heliolites* forms rounded or encrusting masses; further, the smaller tubes which form the cœnenchyma branch dichotomously in *Heliolites*, but in *Heliopora* new tubes are introduced between the older ones. By many writers these two genera are considered to be closely allied, but the relationship is denied by others, who state that important differences are found in the structure of the corallite walls and septa. According to Lindström and others, the corallites of *Heliolites* possess a distinct and independent wall (theca) and also have true septa, whilst in *Heliopora* the corallites are simply bounded by the walls of the cœnenchymal tubes, and possess pseudosepta instead of septa and these have the

form of ridges except at the openings of the corallites. Bourne, on the other hand, considers that the corallites of *Heliolites* possess no independent wall, and agree in this respect with *Heliopora*. Although the cœnenchyma of *Heliolites* resembles closely that of *Heliopora*, yet Lindström and Kiär maintain that it has originated independently in the two genera, and cannot be taken as evidence of relationship; this view is based on a study of the development and phylogeny of *Heliolites*, and leads to the conclusion that that genus and its allies constitute a specialised offshoot from the early Rugosa; it is claimed that *Heliolites* has descended from an earlier Heliolitid in which the cœnenchyma is vesicular instead of tubular, and that the circular corallite wall of the Heliolitids is equivalent to the inner circular wall of *Acervularia* and *Endophyllum*, whilst the cœnenchyma represents the vesicular dissepiments of those genera. The great interval of time between the last appearance of *Heliolites* and first appearance of *Heliopora* lends support to the view that these genera are not closely allied; the former and its allies are not known in rocks of later age than the Devonian, while the latter has been recorded in rocks of Cretaceous and later date only.

Plasmopora. Allied to *Heliolites*. Usually discoidal or hemispherical. Walls of smaller tubes incomplete or absent, and their tabulæ forming a vesicular tissue. Septa in corallites lamellar, and prolonged outside each calyx, so as to enclose large spaces of uniform size. Basal epitheca with concentric ridges. Ordovician to Devonian. Ex. *P. petaliformis*, Silurian.

Propora. Allied to *Plasmopora*. Edges of calyces projecting; septa represented by spines, and not prolonged outside the calyx to enclose large spaces. Ordovician to Silurian. Ex. *P. tubulata*, Wenlock Limestone.

Halysites. Compound; corallites long and tubular, arranged in a single row and united at their sides so as to form laminæ, which intersect; in some species the corallites are of two sizes—the smaller perhaps represent the cœnenchymal tubes of *Heliolites*. Epitheca thick. Septa absent or represented by spines. Tabulæ well developed, horizontal or concave. Llandeilo Beds to Wenlock Limestone. Ex. *H. catenularia*, Wenlock Limestone.

Chætetes. Massive, often laminar, consisting of slender, tube-like polygonal corallites which are contiguous; walls perforated.

Tabulæ well-developed, widely separated. Septa represented by a single row of spine-like processes on one side of each corallite. Chiefly Carboniferous. Ex. *C. radians.*

Distribution of the Anthozoa

Zoantharia. From the point of view of their distribution at the present day, the Madreporaria may be divided into two groups, the solitary and the reef-building.

The solitary corals (*i.e.* the corals which do not form reefs) are found in almost all latitudes, but live mainly in rather deep water, the larger number occurring between depths of 50 and 1000 fathoms; some few (*e.g. Caryophyllia*) live in quite shallow water, whilst others inhabit the depths between 1000 and 2900 fathoms. The species of solitary corals have a wide distribution, being apparently but little affected by conditions of temperature and depth. It might therefore be expected that they would also have a long range in time; this however is not the case, for existing species extend but a short way back into the geological record, and not a single living form is found fossil in the English Cainozoic formations; about a third of the living genera, however, are represented in Cainozoic rocks, and a few (*e.g. Caryophyllia, Parasmilia, Trochocyathus*) occur in Mesozoic formations, but none range into the Palæozoic.

The distribution of the reef-building corals, unlike that of the solitary forms, is limited by both depth and temperature. Thus they are found only in shallow water, not usually extending lower than 20 or 30 fathoms, and only where the temperature of the ocean is not less than 65° F.; they flourish only in water warmer than this. Like the solitary corals, the reef-building genera of the present day have but a very limited geological range, only a very few extending back so far as the Mesozoic period.

Corals, with possibly one or two exceptions, can only exist in salt water; but *Madrepora cribripora* is said to inhabit nearly fresh water. Clear water is likewise generally necessary, but one species, *Porites limosa,* thrives in muddy situations. In geological times, and especially in the Palæozoic and Mesozoic periods, the reef-building corals had a much wider geographical range than they have at the present day, and their remains occur abundantly in various formations in both temperate and polar regions; but in the course of the later Cainozoic period the range of the reef-builders became more and more restricted until the present limits were reached.

With perhaps a few exceptions the Zoantharia found in the Palæozoic formations belong to the Rugose group. The other common corals of the Palæozoic belong to the Tabulate group, the systematic position of which is uncertain. In the Mesozoic and later formations Aporose and Perforate corals are abundantly represented.

Alcyonaria. The Alcyonaria occur in all parts of the world, and are found at all depths from the shore-line down to 2300 fathoms, but they are most abundant at depths of less than 100 fathoms; beyond this limit the number of species gradually diminishes as the depth of the water increases.

Very few of the modern Alcyonarian families occur fossil, but the Pennatulidæ are represented in the Trias by *Prographularia,* in the Lower Lias by *Mesosceptron,* in the Cretaceous by *Pavonaria,* and in the Cainozoic by *Graphularia.* The red coral, *Corallium,* is found in the Cretaceous and Cainozoic (perhaps also in the Jurassic); forms allied to *Gorgonia* occur in the Cretaceous and Tertiary rocks; *Isis* is found in the Cainozoic, and perhaps also in Cretaceous formations. Spicules, similar to those of *Alcyonium,*

have been detected in the Upper Cretaceous. *Heliopora* is first recorded from the Cretaceous. The organ-pipe coral, *Tubipora*, has not been found fossil.

Fossil corals are comparatively rare in argillaceous and arenaceous beds but often abundant in calcareous rocks, many limestones being formed almost entirely of coral remains. This is indeed what might be expected, since existing forms can, as a general rule, live only in clear water. The chief features in the geological distribution of the Anthozoa are given in the following table.

Cambrian. A few genera which may be corals have been found in the Cambrian in North America, Sardinia and Spain.

Ordovician. In North America corals (especially *Streptelasma*) are common in this system, but in England only a few forms have been found, the most important being *Favosites*, *Heliolites*, *Halysites*.

Silurian. Corals are very abundant, especially in the Wenlock Limestone. *Cyathophyllum*, *Acervularia*, *Omphyma*, *Lindstrœmia*, *Goniophyllum*, *Syringopora*, *Favosites*, *Heliolites*, *Plasmopora*, *Propora*, *Halysites*.

Devonian. *Cyathophyllum*, *Acervularia Phillipsastræa*, *Cystiphyllum*, *Calceola*, *Favosites*, *Pachypora*, *Pleurodictyum*, *Heliolites*.

Carboniferous. *Cyathophyllum*, *Lithostrotion*, *Clisiophyllum*, *Dibunophyllum*, *Aulophyllum*, *Lonsdaleia*, *Zaphrentis*, *Cyathaxonia*, *Caninia*, *Amplexus*, *Cleistopora*, *Michelinia*, *Syringopora*.

Permian. Only a very few forms have been found.

Trias. Corals are absent in England, but abundant in the Alpine Trias; most of the Palæozoic forms have become extinct and in place of them are *Rhabdophyllia*, *Cladophyllia*, *Montlivaltia*, *Thecosmilia*, *Isastræa*, *Phyllocœnia*, *Astrocœnia*, *Stylina*, *Omphalophyllia*.

Jurassic. *Montlivaltia*, *Isastræa*, *Thamnastræa* and *Thecosmilia* are found in the Lias but are not common; in the Oolites they become very abundant and several other genera also occur, *e.g.* *Stylina*, *Cyathophora*, *Cladophyllia*, *Calamophyllia*, *Anabacia*.

Cretaceous. Corals are not abundant in England; the chief forms are *Parasmilia*, *Trochocyathus*, *Micrabacia*, *Holocystis*. In some parts of Europe, especially in the Gosau beds (of Chalk age) of the Austrian Alps, corals are very numerous and include *Astrocœnia*, *Montlivaltia*, *Isastræa*, *Cyclolites*, *Thamnastræa*, etc.

Cainozoic. Corals are rare in English Cainozoic formations: *Turbinolia*, *Dendrophyllia*, *Oculina* and *Goniopora* (*Litharæa*) occur in the Eocene; *Madrepora* in the Oligocene; *Flabellum* in the Pliocene. In the middle and south of Europe, and in the south-eastern part of the United States, corals are found abundantly in various Cainozoic deposits.

PHYLUM ECHINODERMA

Sub-Phyla.	*Classes.*
1. Eleutherozoa	1. Asterozoa.
	2. Echinoidea.
	3. Holothuroidea.
2. Pelmatozoa.........	1. Crinoidea.
	2. Cystidea.
	3. Blastoidea.
	4. Edrioasteroidea.

THE Echinoderms are all marine and comprise the star-fishes, brittle-stars, sea-urchins, sea-lilies, sea-cucumbers, and the extinct blastoids and cystideans. The body is very often radially symmetrical, the symmetry being generally pentamerous. But in many cases there is also a more or less well-marked bilateral arrangement of parts. In the majority of cases the alimentary canal terminates in an anus. A body-cavity or cœlom is present and surrounds the alimentary canal. The water-vascular system (fig. 52) is one of the distinguishing features of the group: it consists of a set of vessels containing a watery fluid and generally placed in communication with the sea-water by means of a canal; one vessel forms a ring round the œsophagus from which radiating trunks are given off. The water-vascular system functions in respiration and as a sensory organ, and generally also in locomotion. A nervous system is present; one part of it has a distribution similar to that of the water-vascular system. Reproduction is mainly sexual; as a rule the sexes are separate, but do not differ externally.

In nearly all echinoderms there is a dermal skeleton.

This is calcareous and consists sometimes of isolated pieces, but more usually of rods or plates united by fibres of connective tissue and forming a complete shell or test, which may be either flexible or rigid; spines and other processes are often attached to the plates. When examined microscopically each part of the skeleton is found to be formed of a network of calcareous rods (fig. 49), with a jelly-like substance in the spaces of the network. The details of the

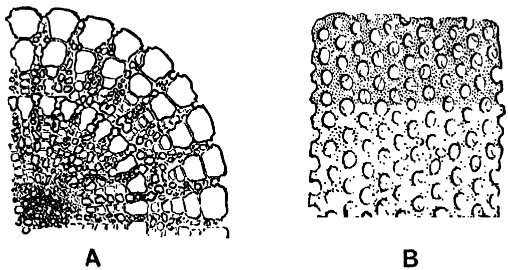


Fig. 49. A. Portion of transverse section of a spine of a sea-urchin, *Echinometra*, Recent. Magnified. B. Section of interambulacral plate of recent *Cidaris* cut parallel to the surface. Magnified.

structure vary in different forms, depending on the size and shape of the spaces between the rods. In the spines of sea-urchins the network of rods has usually a radial arrangement, with polygonal or rectangular spaces (fig. 49 A), except at the centre, where the structure is more irregular. Another characteristic feature of the skeleton is that each component part shows the optical characters of a crystal of calcite, and differs only from an ordinary crystal in not having crystal contours and in the possession of the netted structure. In a plate the principal crystallographic axis is at right angles to the surface, in a spine it is parallel with the length. In fossil specimens the spaces in the network of rods usually become filled with calcite, which is deposited

in crystalline continuity with that forming the plate or spine. In such cases the characteristic cleavage of calcite becomes well marked, so that when the plate or spine is broken, the fracture passes along the cleavage planes, instead of being irregular as in the recent forms. By the infiltration of calcite and the development of cleavage, the organic structure in fossil echinoderms is sometimes partly or almost completely destroyed.

The Echinoderma are divided into two main groups, (1) the Eleutherozoa, (2) the Pelmatozoa.

I. ELEUTHEROZOA

The Eleutherozoa possess no fixing organ and are able to move about freely. This group is divided into three classes:—(1) Asterozoa, (2) Echinoidea, (3) Holothuroidea.

CLASS I. ASTEROZOA

The Asterozoa are represented in the older Palæozoic rocks by a great diversity of forms, but these, in the main, can be arranged in two groups which have survived to the present day—the Asteroidea (or starfish) and the Ophiuroidea (or brittle-stars). The Asteroidea are the simpler of these two groups, and have undergone less modification from the parent Asterozoan stock. All the forms of the Asterozoa are built round the water-vascular system (fig. 52) in a more or less similar way; there is a central mouth inside the water-vascular ring, and a disc of varying extent around the mouth; five arms (occasionally secondarily multiplied) come off from the disc. The main variations in the structure of the skeleton appear to be connected with the manner of life of the forms, and can be best illustrated by an account of the structure of the two groups.

SUB-CLASS I. ASTEROIDEA

In the Asteroidea the arms are usually short and merge gradually into the disc. Occasionally, as in the recent genus

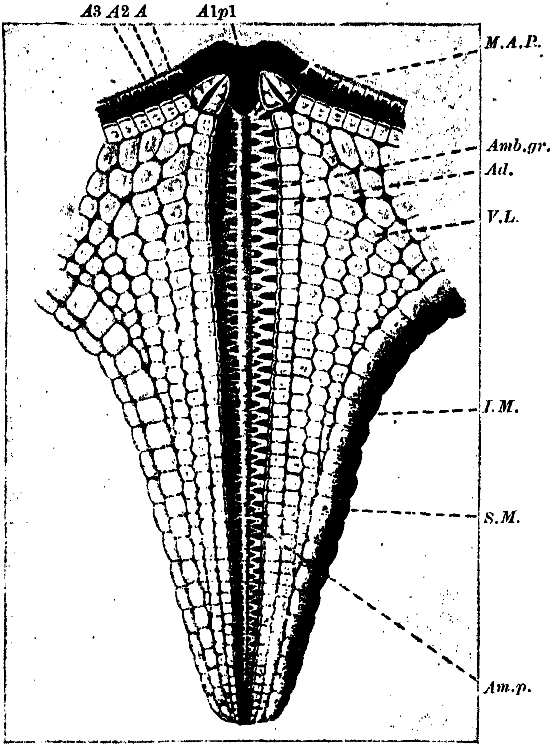


Fig. 50. Oral surface of a fifth part of the skeleton of *Pentaceros reticulatus*. *A1pl*, anterior process of first ambulacral; *A*, *A2*, *A3*, the first three ambulacral ossicles; *M.A.P.*, mouth-angle plates; *Amb.gr.*, ambulacral groove; *Ad.*, adambulacrals; *V.L.*, ventro-lateral plates; *I.M.*, infero-marginal ossicles; *S.M.*, supero-marginal ossicles; *Am.p.*, ambulacral pore. (From Spencer after Agassiz.)

Pentagonaster and in the Chalk genus *Metopaster*, the arms are so short that the whole body is almost a pentagon.

Other genera, such as *Astropecten*, have longer arms, but no Asteroidea, except a few deep sea forms, have the long thin arms which usually characterise the Ophiuroidea.

The two surfaces of the Asteroid are readily distinguishable. The under surface (known as the *oral*, *ambulacral*, *actinal* or *ventral*, fig. 50) is marked by the mouth, and the five deep ambulacral grooves (*Amb. gr.*) along the arms.

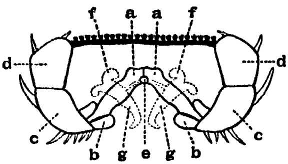


Fig. 51. Section of the arm of a star-fish (*Astropecten*). *a*, ambulacral ossicles; *b*, adambulacral plates; *c*, inferomarginal plates with spines; *d*, supero-marginals; *e*, radial water vessel; *f*, ampulla; *g*, tube-feet. Enlarged.

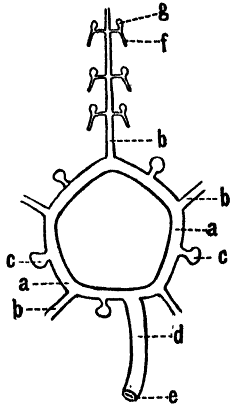


Fig. 52. Diagram of the water-vascular system of a star-fish. *a*, circular vessel round the mouth; *b*, radial vessels; *c*, Polian vesicles; *d*, stone-canal; *e*, madreporic plate; *f*, tube-feet (only a few shown); *g*, ampulla.

In each of these grooves one of the five radial water vessels (52 *b*) is placed and from it arise the tubular offshoots known as the *tube-feet* (*f*). The upper surface (known as the *apical*, *aboral*, *antiambulacral*, *abactinal* or *dorsal*) is completely covered over; a distinct ossicle on this surface is the *madreporite*, the porous plate through which water is admitted into the water-vascular system.

The ambulacral grooves extend from the mouth to the

extreme tip of the arms. Each groove is formed by two rows of ossicles (the *ambulacral ossicles*, fig. 51 *a*) which meet at an angle making an arch, and is bordered on each side by another row of ossicles, the *adambulacrals* (fig. 51 *b*). Between the ambulacrals are pores for the passage of the *ampullæ* or reservoirs (*f*) attached to the tube-feet (*g*). The tube-feet themselves are used for pulling open Lamellibranchs on which star-fish feed, and for climbing and walking. The ambulacral groove can be closed for the protection of the tube-feet by muscles placed ventrally to the radial water vessel or opened by muscles dorsal to the same structure. Longitudinal muscles occur between the adambulacrals and at the dorsal tips of the ambulacral ossicles, by means of which each side of the arm can be contracted. The ossicles nearest the mouth, in series with the adambulacrals, are called *mouth-angle plates* (fig. 50, *M.A.P.*); they are often so stout that they give the mouth a star-shaped form. In the inter-radial angles supporting the mouth-angle plates is a stout plate, the *odontophor*; this is not usually visible on the oral surface in recent forms as it is covered by the ventro-lateral plates, but in many Palæozoic genera which do not possess ventro-laterals it is seen distinctly.

In the remaining parts of the skeleton, which are known collectively as the *interambulacral skeleton*, the following parts are usually clearly differentiated.—(1) a double series of plates, the *supero-* and *infero-marginals* which form the sides of the arms and disc (figs. 51 *c*, *d*, 50 *S.M.*, *I.M.*): (2) small plates, the *ventro-laterals* placed on the oral surface of the disc between the marginal plates and the adambulacral ossicles (fig. 50 *V.L.*): (3) a central primary circlet of radial and inter-radial plates on the aboral surface, usually more distinct in the young than in the adult form: (4) plates which fill in the remaining portions of the aboral surface.

The plates running down the middle of the aboral surface of the arm are known as radials. The terminal member of this series is notched for the reception of the most distal tube-foot which possesses an eye-spot, and the plate is therefore known as an *ocular*. Some or all of the plates of the interambulacral skeleton may be partly cut away to allow of tube-like projections of the skin which form simple respiratory organs known as *dermal branchiæ* or *papulæ*.

All the plates except the ambulacrals may carry spines. The disposition of the spines is of importance in classification. In the genera found in the Chalk the ornament formed by the pits in which the spines are sunk may be used to distinguish genera and even species. Frequently some of the spines are modified into pincer-like organs (*pedicellariæ*) which serve for protection and as a means of cleaning the surface of the body.

The soft parts follow the general radiate symmetry already noticed in the water-vascular system. The mouth leads into a short œsophagus which opens into a globular stomach; above the stomach is the pentagonal pyloric sac, from the angles of which are given off branches which soon divide into two and extend down the arms near the aboral surface. From the pyloric sac a short narrow intestine leads to the anus at the centre of the aboral surface. The distribution of the main part of the nervous system is similar to that of the water-vascular system: it consists of a ring round the mouth and of a branch which extends down the ambulacral groove of each arm; there is also a layer of fine nerve fibres under the ectoderm. The genital glands occur in pairs at the base of each arm and open to the exterior between the rays. The water-vascular system communicates with the exterior by means of a canal (fig. 52 *d*) which passes from the circular vessel to the madreporite on the

aboral surface of the disc; this is known as the *stone canal* on account of the deposit of carbonate of lime in its walls.

Metopaster. Body flattened, pentagonal in outline, the rays only slightly produced. Marginal plates thick, with rabbet edge which bears shallow spine pits. Supero-marginal plates few in number, forming a broad border to the disc; the terminal pair of plates the largest. Aboral surface covered with small polygonal (usually hexagonal) plates. Infero-marginal plates more numerous than the supero-marginals. Plates on the oral surface small, polygonal. Cretaceous. Ex. *M. parkinsoni*, Upper Chalk.

Mitraster. Similar to *Metopaster*, but rounded (or slightly pentagonal) in form, with supero-marginal plates few and of more nearly equal size. Chalk. Ex. *M. hunteri.*

Crateraster. Body almost pentagonal. Lateral faces of marginal plates with crater-like pits. Apical faces of marginals usually with rugosities. Chalk. Ex. *C. quinqueloba.*

Pycinaster. General shape of the body similar to *Calliderma.* Marginals high and almost smooth. Supero-marginals wedge-shaped. Upper Greensand and Chalk. Ex. *P. angustatus*, Upper Chalk.

Calliderma. Body flattened, pentagonal-stellate, with the rays moderately long. Marginal plates large, forming a broad border to the disc, covered with shallow spine pits. Aboral surface of disc with small plates arranged regularly. Cretaceous to present day. Ex. *C. smithiae*, Chalk.

Stauranderaster. Body high; arms produced. Plates with a rabbet edge. Ornament on plates, when present, confined to the central raised area. Proximal marginals breast-plate shaped. A distinct central circlet of plates is often present on the aboral surface. Chalk. Ex. *S. bulbiferus.*

SUB-CLASS II. OPHIUROIDEA

The Ophiuroidea are a highly modified group. The arrangement of the nervous and water-vascular systems is similar to that found in the Asteroidea, but the tube-feet no longer have any locomotory function, being merely sensory or respiratory organs. The arms are long and thin, and are

capable of wriggling and writhing movements. The disc is round and sharply marked off from the arms. Many Ophiuroids live on mud from the sea bottom which they push into their mouths by means of the tube-feet nearest the mouth.

The structure of the arm is shown in fig. 53. The ambulacral ossicles are no longer pairs of rod-like bodies, but consist of a single series of stout *vertebræ* (fig. 53 *d*) which articulate upon each other. The derivation of these vertebræ from pairs of ambulacral ossicles can be followed in the young forms and in the older Palæozoic fossils. The adambulacrals are represented by thin plates, known as lateral plates or side shields (*b*), which usually possess a ridge carrying a comb of long spines. The aboral surface is protected by a series of dorsal plates (*a*) analogous to the radials of the Asteroidea. The groove is covered by ventral plates (*c*) not represented in the Asteroidea. Neither generative organs nor diverticula from the alimentary canal enter the arms as they do in the Asteroidea.

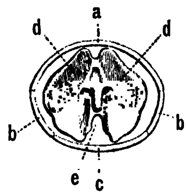


Fig. 53. Section of the arm of an Ophiuroid (*Ophioglypha*). *a*, dorsal plate; *b*, lateral plate; *c*, ventral plate; *d*, ambulacral ossicles fused along the median vertical line; *e*, ambulacral groove. Enlarged.

The oral surface of the disc (fig. 54 A) is formed by inter-radial pouches covered with scaly plates and granules. The slits (*g*) between the pouches and the arms serve as genital openings and for the entrance of water for respiratory purposes. In the inter-radial angles between the mouth plates are five large *buccal plates* (*b*), one of which serves as a madreporite. The aboral surface of the disc (fig. 54 B) is in most cases covered with numerous small plates, but usually there is at the bases of the arms on each side a

large plate, the *radial* (*r*). Some forms have a primary circlet of plates similar to that mentioned for the Asteroidea (p. 116).

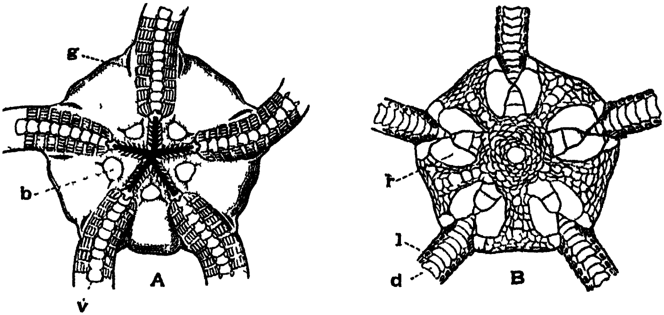


Fig. 54. A. *Ophiura*, Recent. Oral surface of disc and part of the arms. *b*, buccal plates; *g*, genital slits; *v*, ventral plates of arms. B. *Ophioglypha*, Recent. Aboral surface. *r*, radial plates; *l*, lateral plates of arms; *d*, dorsal plates of arms. $\times 1\frac{1}{2}$.

The mouth-angle plates are fused with the proximal pair of ambulacrals to form stout jaws. A single stout plate, the *torus*, situate at the mouth extremity of each pair of jaws carries strong spines or teeth which are used for grinding.

The Palæozoic Ophiuroidea differ from recent forms in several respects. All the best known forms are devoid of ventral plates covering the groove. The radial water vessels are protected by outgrowths of the ambulacral ossicles which form a closed canal. The opposite members of each pair of ambulacral ossicles are not fused into single vertebræ. There are no buccal plates, and the madreporite is a separate plate. The vertebræ of some genera possess articulating knobs and prominences similar to those in recent forms The principal Palæozoic genera are:

Lapworthura. Disc circular, composed of small spicules. The halves of each vertebra (ambulacrals) are opposite. Ludlow Beds. Ex. *L. miltoni*.

Aspidosoma. Disc with concave edges, bordered by a single row of marginal plates. Ambulacral plates alternating. Ordovician to Devonian. Ex. *A. petaloides*, Devonian.

Protaster. Disc composed of overlapping scales. Ambulacral ossicles alternating. Silurian. Ex. *P. sedgwicki*, Ludlow Beds.

Distribution of the Asterozoa

The Asteroidea have a wide distribution in the ocean at the present day; they are most abundant at moderate depths, but also occur in abyssal regions.

The majority of the Ophiuroids live in shallow water, more than half of the known species being found at a depth of less than 30 fathoms, and most of these not extending lower. Other forms occur at greater depths, some species being found below 1000 fathoms.

The earliest representatives of the Asterozoa at present known are found in the Middle Ordovician. Complete specimens are usually rare as fossils since the skeleton readily breaks up after death, but at some horizons and localities numerous examples have been found, viz.:—Upper Ordovician of Thraive Glen, Girvan; Wenlock Beds of Gutterford Burn, Pentland Hills; Lower Ludlow of Leintwardine, Herefordshire; Lower Devonian (Budenbach Slates) of the Rhine; Lias of Whitby and Lyme Regis; Corallian (Calcareous Grit) of Yorkshire; Upper Chalk of Bromley, Kent.

The classification of the fossil Asterozoa is not yet settled. The following Palæozoic genera are closely allied to the recent Asteroidea—*Hudsonaster*, *Mesopalæaster*, and *Promopalæaster* (Ordovician and Silurian), *Xenaster* and *Devonaster* (Devonian); these genera show, to some extent, characteristics found in the young of recent forms, for they usually possess a comparatively simple skeleton and have a very distinct primary circlet of plates in the centre of the aboral surface of the disc.

An extinct branch of the Asteroidea is formed by the Palæozoic genus *Urasterella* and its allies; the disc of these forms is small and the arms are long and thin; the adambulacral plates are broad and possess a distinct ridge which bore stout Ophiuroid-like spines.

Some Palæozoic Asterozoa have an Asteroid shape and Asteroid-like ambulacrals, but the madreporite, when known, is on the oral surface, and they show other peculiarities of structure which ally them with the Ophiuroidea rather than with the Asteroidea; these include *Stenaster* (Ordovician), *Schuchertia* (Ordovician and Silurian), *Helianthaster* (Devonian), *Palasteriscus* (Devonian), *Sturtzaster*, *Rhopalacoma* and *Bdellacoma* (Lower Ludlow).

Well-known Palæozoic Ophiuroids are *Lapworthura* (Ludlow), *Aspidosoma* (Ordovician to Devonian), *Protaster* (Ludlow), and *Onychaster* (Devonian and Carboniferous).

Forms very similar to living Ophiuroids are found in the Jurassic and have been referred to the recent genera *Ophiura*, *Ophiolepis*, and *Ophiocten*. In the Cretaceous *Ophiura* and *Amphiura* occur. A few forms, such as *Ophioglypha*, have been found in the Eocene.

The Asteroidea in the Jurassic formations closely resemble living forms and have been referred to the genera *Astropecten*, *Solaster* and *Plumaster*. The Asteroidea of the Cretaceous are found chiefly in the Chalk where isolated marginal plates are often abundant and can be used for the determination of zonal horizons; the principal genera are *Metopaster*, *Mitraster*, *Crateraster*, *Pycinaster*, *Calliderma* and *Stauranderaster*. In the Cainozoic rocks of England star-fishes are rarely found.

CLASS II. ECHINOIDEA

The echinoids or sea-urchins have usually a globular, heart-shaped, or discoidal body, covered with spines. The shell or test is covered by a layer of ectoderm and consists of numerous calcareous plates, which, in the majority of cases, are immovably united. Nothing corresponding to the ambulacral groove of the star-fish is to be seen on the surface, since the water-vascular system is internal to the skeleton,

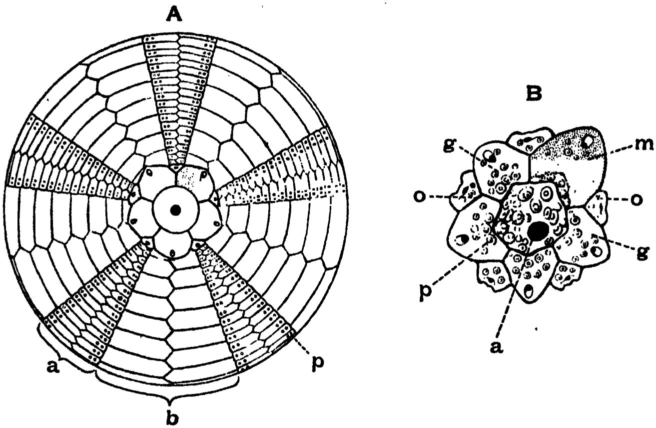


Fig. 55. A. Diagram of the upper surface of a regular echinoid, with the tubercles and spines omitted. *a*, ambulacral areas; *b*, inter-ambulacral areas; *p*, pores in the ambulacral plates.

B. Apical disc of *Echinus esculentus*, Recent. *a*, anus; *p*, periproctal membrane with small plates; *g*, genital plates, each with a pore; *m*, madreporic plate; *o*, ocular plates. × $1\frac{1}{3}$.

and as a result the tube-feet, in order to reach the exterior, must pierce the plates of the test. With one exception the mouth is always on the inferior surface; it is either central or placed in front of the centre. The anus is either at the summit of the test or posterior to it, somewhere along a line drawn from the summit to the centre of the base. In the regular echinoids both anus and mouth are central

—being placed at opposite poles of the test; in the irregular echinoids the anus is always, and the mouth often, excentric. In the test we may distinguish three parts: a small patch of plates placed at the summit, known as the *apical disc* or *apical system*; the main part of the test termed the *corona*; and the part between the mouth and the lower margin of the corona, which usually bears plates and is known as the *peristome*.

In a typical echinoid of the regular group (*e.g. Echinus*) the anus is placed within the apical disc (fig. 55 B), which then consists of the following parts. Near the centre is the anus (*a*), which is surrounded by a membrane bearing small plates and known as the *periproct* (*p*). The periproct is encircled by a ring formed of ten plates, five are called *genital* (*g*) and five *ocular* (*o*). The genital plates form the inner part of the ring; they are often more or less hexagonal in outline, and are usually provided with a perforation which serves as the opening for the genital ducts—whence their name; one is pierced by numerous pores and is the madreporic plate (*m*). Outside the genital plates and alternating with them are the ocular plates; these are smaller than the genital and usually triangular or pentagonal, and each has a perforation through which the terminal tentacle of the radial water-vessel projects; this is pigmented and has sometimes been regarded as a rudimentary visual organ[1].

In most of the regular echinoids the apical disc is large, but particularly so in *Cidaris*, *Salenia*, *Peltastes*, and their allies. In a few regular forms (fig. 56 D) the genital

[1] The genital plates are sometimes termed *basals* and the oculars are also known as *radials*, since, by some authors, they have been considered to represent the plates which bear those names in other groups of the Echinoderma. It is more probable that, although occupying similar positions, they have originated independently in the different groups.

plates are completely separated from one another by the oculars, so that a single row of ten plates encircles the periproct; in others, some only of the genital plates are separated by oculars. Each genital plate has usually one perforation only, but in many Palæozoic forms (fig. 56 D) there are three or more, and in *Cidaris* often two. Similarly the oculars in a few Palæozoic echinoids have two perforations instead of one. In *Salenia* and *Peltastes* there is an extra plate in the apical disc; it is in front of the periproct and is known as the *sur-anal* plate (fig. 56 A, *b*).

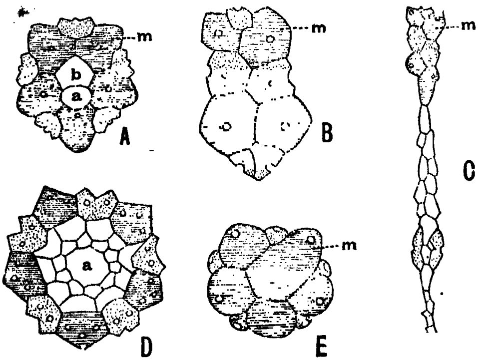


Fig. 56. Some types of apical disc. A. *Peltastes wrighti*, Lower Greensand. B. *Echinocorys vulgaris*, Upper Chalk. C. *Collyrites bicordata*, Corallian. D. *Palæechinus*, Carboniferous Limestone. E. *Galerites subrotundus*, Chalk. In the figures the ocular plates are distinguished by dots, the genital plates by lines. *m*, madreporic plate; *a*, anus; *b*, sur-anal plate. All enlarged.

In the irregular echinoids the apical disc is small, since it does not enclose the periproct. The madreporic plate may extend to the centre of the disc (fig. 56 E, *m*), and sometimes (*Spatangus*) reaches to the posterior border, separating the posterior oculars. The posterior genital is sometimes absent (fig. 56 B), and when present may be without a perforation (E). In *Echinocorys* and *Holaster* the apical disc is elongated, and the anterior genitals are

separated from the posterior genitals by two oculars which join in the middle (fig. 56 B); in *Collyrites* (C) the apical disc is still more elongated, since the two posterior oculars are separated from the rest of the apical disc by a chain of small plates.

The corona in a typical echinoid consists of twenty columns of plates, each column extending from the apical disc to the peristome. The plates are of two kinds, *ambulacral* (fig. 55 A, *a*) and *interambulacral* (*b*); there are five double columns of ambulacrals separated by five double columns of interambulacrals; each double column is termed an *area*. The former end against the ocular plates, the latter against the genital, and in each case fresh plates are developed next the apical disc. In each area the plates alternate on either side, and since their inner ends are angular, the line between the two rows is zig-zag.

The ambulacral plates are smaller and more numerous than the interambulacral, and they are perforated by pores (*p*) for the passage of the tube-feet to the exterior, a radial water-vessel being placed under each ambulacral area. The pores are usually round, but sometimes elongated; in most cases they are situated in the outer portion of the plates and are almost always in pairs; each pair of pores corresponds to a single tube-foot, since each tube-foot divides at its base into two canals. Frequently each pair of pores is surrounded by an oval raised rim, the *peripodium* (fig. 57); the two pores in each pair are sometimes horizontal, but usually inclined so that the inner pore is lower than the outer pore. In some echinoids, such as *Cidaris*, and all the Palæozoic genera, each ambulacral plate is formed of one piece only (as in fig. 55)—such plates are called *simple*. In other cases some of the ambulacral plates

are *compound,* consisting of two, three or more small plates which have become fused together; but the original plates are still indicated by the lines of suture between them and also by the pair of pores on each (fig. 57); in some genera (fig. 57 A) the plates which are united are all *primaries*—that is to say, each extends from the margin to the middle line of the ambulacral area; but frequently some of the plates taper away and do not reach the middle line (or inner edge of the compound plate)—such are called *demi-plates* (*e.g.* the middle plates in fig. 57 B). This fusion of plates is usually stated to be due to growth-pressure—since each plate of the test is enlarging and

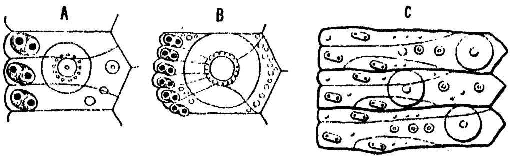


Fig. 57. **Compound Ambulacral Plates. A.** ***Pseudodiadema hemisphæricum,*** **from the Corallian, formed of three fused plates. B.** ***Phymosoma koenigi,*** **from the Chalk, formed of six fused plates. C.** ***Stomechinus perlatus,*** **Upper Jurassic, three plates, each formed of three fused plates, with trigeminal pores. Enlarged.**

new plates are being added next the apical disc; the fact that some of the fused primary plates are smaller than others, and also the presence of demi-plates, is attributed to the reduction in size of the original plates by the absorption of material under pressure. The difference in size may, however, be due mainly to the more rapid superficial growth of the plates on which large tubercles are developed. The pores in the ambulacra of some echinoids are placed one immediately above the other, so that one vertical row of pore-pairs is seen—such pores are termed *unigeminal* (fig. 55); in other cases the pore-pairs

are alternately near to, and more distant from, the margin of the ambulacral plate, and consequently two vertical rows are formed, and the pores are said to be *bigeminal*; in a similar way three or more vertical rows of pore-pairs may be produced, when the pores are known as *trigeminal* (fig. 57 C) or *polygeminal*. Sometimes the pores in each pair are united by a groove on the surface of the plate, and are then termed *conjugate*. In some sea-urchins the two rows of pores in each ambulacral area diverge rapidly after leaving the apical disc, and then come together again before reaching the circumference (or *ambitus*), so that this part of the ambulacrum is leaf-like, and the five ambulacra together form a rosette on the upper surface of the corona, the pores being either wanting or but irregularly developed on the lower surface; the ambulacral areas in such cases are termed *petaloid* (*e.g.* *Scutella*) but when the rows of pores diverge but do not come in contact at their outer ends they are *sub-petaloid* (*e.g.* *Nucleolites*). When, as in *Cidaris*, the distance between the two rows of pores increases uniformly and slowly in passing from the apical disc to the equator, and the pores are equally well-developed on the under surface of the test, the ambulacra are said to be *simple* (fig. 55).

The advantage gained by the development of compound plates, which appear first in Triassic echinoids, seems to be to give a larger number of tube-feet in each vertical row. The bigeminal or trigeminal arrangement of pores causes the tube-feet to be spread over a larger area, and so increases their mechanical efficiency; the same result was attained by the development of numerous columns of plates in Palæozoic echinoids (see below). Petaloid ambulacra are particularly well-developed in flattened or cake-like echinoids, and in such forms the tube-feet have for the

most part lost their locomotory function and have become respiratory organs.

With only a few exceptions the corona in the Mesozoic and later echinoids is formed of twenty columns of plates, as described above; but in the Palaeozoic echinoids, more than twenty columns of plates are found (fig. 61), except in the earliest-known genus *Bothriocidaris* (Ordovician), which is remarkable in having only one column of plates in each interambulacral area, with the usual two columns in each ambulacral area. In other Palaeozoic forms the number of columns is variable and often great, so that the total number of plates in the corona becomes considerable: thus, *Archaeocidaris* possesses two columns in each ambulacrum, and four in each interambulacrum; *Oligoporus* has four ambulacral and from four to nine interambulacral columns; *Melonechinus,* six to twelve ambulacral, and from three to eleven interambulacral columns; whilst *Lepidesthes* consists of from eight to as many as eighteen ambulacral, and three to seven interambulacral columns. In these Palaeozoic forms each ambulacral plate possesses one pair of pores.

In most echinoids the plates join by a vertical suture and the test is rigid, but in some genera the plates of the corona overlap to a slight extent, giving some flexibility to the test; such is the case in several Palaeozoic genera, and also in a few later forms, especially *Pelanechinus* from the Corallian, *Echinothuria* from the Chalk, and some living species of the deep-sea *Asthenosoma* and *Phormosoma.*

The plates of both the ambulacral and interambulacral areas are often provided with rounded elevations known as *tubercles* and *granules.* The tubercles are of various sizes, the largest being the *primary,* and those of smaller

size the *secondary*. In a primary tubercle the following parts may be distinguished: at the summit a hemi-spheroidal piece, sometimes perforated at the top, and known as the *mamelon* (fig. 58 B, *m*). The mamelon rests on the *boss* (*b*), the upper margin of which is sometimes smooth, sometimes crenulated. The base of the boss is frequently surrounded by a smooth excavated space, the *areola* or *scrobicule* (*a*), to which muscles from the spine are attached. The granules are smaller than the tubercles and have no distinct mamelon.

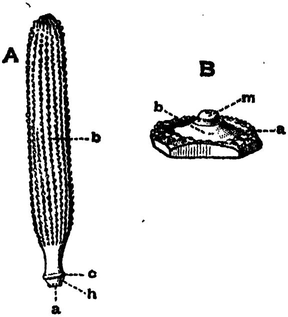


Fig. 58. A. Spine of *Cidaris florigemma*, from the Corallian Rocks. *a*, acetabulum; *h*, head or base; *c*, collar; *b*, shaft or stem. B. Ambulacral plate of *Cidaris* (recent) with a large primary tubercle and secondary tubercles. In the primary tubercle, *m*, mamelon; *b*, boss; *a*, areola. Natural size.

Attached to the tubercles are the *spines* or *radioles*; these are of different sizes and shapes in different genera and species and even on the same individual, being needle-like, rod-like, flask-shaped, etc.; the larger spines are attached to the primary tubercles, the smaller to the secondary tubercles. They serve for protection and also assist in locomotion. At the end of the spine, where it articulates with the mamelon, there is a rounded cavity, the *acetabulum* (fig. 58 A, *a*); next comes the *head* (*h*) limited above by a ring or collar (*c*), which may be smooth or crenulated and serves for the attachment of the muscles that move the spine. Beyond the collar and forming the greater part of the spine is the *shaft* or *stem* (*b*), which may be smooth, or ornamented with ridges or rows of spiny processes. The microscopic structure of the spines

(fig. 49 A) varies in different genera, and is of importance in classification. Pedicellariæ (p. 117), which consist of a stalk with usually three blades, also occur, but are rarely found fossil.

On the surface of some irregular sea-urchins belonging to the sub-order Spatangina (p. 139) there are bands which appear to be nearly smooth, but are covered with very minute tubercles; in the living state they bear slender modified spines. These bands are termed *fascioles*, and their position varies in different genera; sometimes they form a ring beneath the anus (*e.g. Micraster*, fig. 59, *c*), when they are said to be *sub-anal*; in other cases they encircle the rosette formed by the petaloid ambulacra (*e.g. Hemiaster*) and are said to be *peripetalous*; or they extend round the margin of the test (*e.g. Cardiaster*).

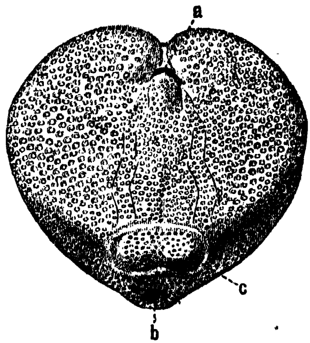


Fig. 59. Under surface of *Micraster cor-anguinum* from the Upper Chalk, showing fasciole. *a*, peristome; *b*, periproct; *c*, fasciole. × ¾.

On the lower surface of the test is the *peristome* (figs. 59, *a*, 60), in the centre of which is the mouth. The peristomal membrane, which extends from the mouth to the edge of the corona, is sometimes (*e.g. Cidaris*, fig. 60) completely covered with rows of plates, but more usually bears small isolated plates only, or is without plates; some of the plates may be perforated and have been derived from the ambulacral areas; others are not perforated. The plates on the peristomal membrane are usually lost in fossil specimens. The peristome varies in shape, size, and position in different

genera; it may be circular, oval, pentagonal, or decagonal; its margin is entire in Palæozoic echinoids and in the Cidaridæ, but in other regular echinoids and in the Holectypina there are ten notches or incisions, by which the five pairs of gills or branchiæ pass to the exterior. The peristome is usually larger in the regular than in the irregular echinoids. In some irregular echinoids belonging to the sub-order Spatangina (p. 139) the parts of the

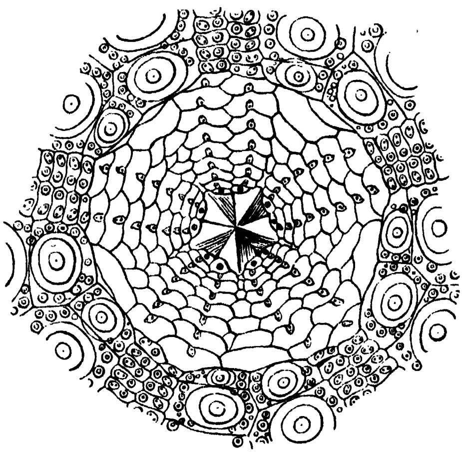


Fig. 60. *Cidaris hystrix*, Recent. Peristome and margin of corona. (After Lovén.)

ambulacra near the peristome are depressed and leaf-like, with the pores close together, whilst the intervening inter-ambulacra are convex; this part of the corona has consequently a petaloid appearance, and is known as the *floscelle*.

A pyramidal or conical structure which functions in mastication, and is known as Aristotle's lantern, is found in regular echinoids and in some irregular forms (Holectypina and Clypeastrina). The lantern consists usually of 40 calcareous pieces including five teeth which project

through the mouth: numerous muscles are attached to the calcareous parts, some of which serve to open or close the teeth and are attached to ridges at the margin of the peristome—these ridges constitute what is known as the *perignathic girdle.* This may consist of ridges arising from the interambulacral plates only, or there may be also processes from the sides of the ambulacral plates, and these often unite, forming an arch or *auricle* over each ambulacral area at the margin of the peristome. The first part of the alimentary canal passes through the axis of the lantern. The circular vessel of the water-vascular system forms a ring round the œsophagus at the top of the lantern, and gives off five radial branches which pass through the auricles and up the middle of the inside of each ambulacral area; lateral branches, which alternate on either side, come off from the radial vessels and open into the tube-feet. The stone canal (p. 117) passes from the circular water vessel to the madreporic plate.

In the irregular echinoids there is a well-marked bilateral symmetry; a plane which passes through the anus (which is in the posterior interambulacral area), the apical disc, and the mouth, divides the body into two similar parts. The ambulacra in these forms often differ considerably in size, and, to some extent in structure; the anterior one may be smaller than the others and frequently has a different arrangement of pores and plates, while the four other ambulacra are paired. The interambulacra are also unlike—the posterior one often forming a large part of the base of the test. The bilateral character is inconspicuous in the regular sea-urchins, but the plane of symmetry may be found by means of the madreporic plate, which is always at the summit of the right anterior interambulacral area.

The Echinoidea may be divided into two Orders, (1) Regularia, (2) Irregularia.

ORDER I. REGULARIA

The peristome is at the centre of the base, and the anus within the apical disc. The ambulacra are simple. Lantern present in all. The test is circular in outline.

Palæechinus (fig. 56 D). Test spheroidal or elliptical, rigid. Apical disc with five large genital plates, each with two to five perforations; ocular plates five, small, separating the genitals. Ambulacra narrow, straight, with two columns of plates; one vertical row of pairs of pores on each side of the area. Interambulacra wide, with four to six columns of plates at the ambitus, fewer towards the poles; plates hexagonal, except those next the ambulacral area, which are pentagonal; surface of plates covered with granules. Spines small. Carboniferous. Ex. *P. ellipticus*, Carboniferous Limestone.

Maccoya. Distinguished from *Palæechinus* chiefly by the ambulacra in the middle part of the test consisting of alternate primary and smaller plates—the latter are nearly or quite cut off from contact with the interambulacral margin; the pore-pairs in this part of the test form two vertical rows. Carboniferous. Ex. *M. intermedia.*

Melonechinus (=*Melonites*) (fig. 61). Test spheroidal, with melon-like ribs from apex to peristome. Apical disc with five genital plates, each having from two to four pores; oculars without pores, separating the genitals. Ambulacra broad, concave on each side of a median ridge, with six to twelve columns of plates, each plate with a pair of pores; four plates at the peristomal edge of each area. Interambulacra consisting of three to eleven columns of small thick plates, which are pentagonal next the ambulacra, hexagonal elsewhere; tubercles very small. Jaws large. Carboniferous. Ex. *M. multiporus.*

Archæocidaris. Test depressed spheroidal, plates overlapping. Ambulacra narrow, sinuous, formed of two rows of plates; pores unigeminal. Interambulacra of four columns of large plates, the middle ones being hexagonal; each plate has a large primary perforated tubercle which bears a long spine, and small tubercles at the

margin. Peristomal membrane covered with plates. Carboniferous and Permian. Ex. *A. urii*, Carboniferous Limestone.

Cidaris (fig. 60). Test spheroidal, the summit and base equally flattened. Apical disc very large, rarely preserved fossil, ocular plates large. Ambulacra narrow, flexuous or nearly straight, plates simple, pores unigeminal; between the rows of pores are vertical rows of small tubercles and granules. Interambulacra wide, plates large, each with a primary tubercle which is perforated, and may be crenulated or smooth; areola large, surrounded by secondary tubercles, beyond which may be granules. Peristome large, without incisions, its membrane covered with plates. Spines large, of various forms, generally ornamented with rows of granules. The term *Cidaris* is here used in the extended sense, and includes several divisions usually regarded as genera. Jurassic to present day; allied forms occur in the Trias. Ex. *C. florigemma*, Corallian and Kimeridgian.

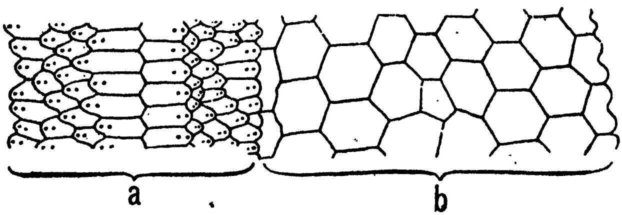


Fig. 61. *Melonechinus multiporus*, Carboniferous. Part of an ambulacral area (*a*) and an interambulacral area (*b*) from the equator of the test. Based on figures given by Jackson. × 2.

Peltastes (fig. 56 A). Test small, circular in outline, depressed. Apical disc very large, prominent, with a sur-anal plate in front of the periproct; the madreporic plate has an oblique fissure. Ambulacra narrow, straight or slightly flexuous, with small tubercles; pores unigeminal except near the peristome; plates, primaries. Interambulacra wide, with large primary tubercles, which are imperforate, but may be crenulate. Peristome slightly notched. Upper Jurassic to Chalk. Ex. *P. wrighti*, Lower Cretaceous.

Salenia. Similar to *Peltastes*, but the periproct is on the right of a median line drawn from the anterior to the posterior margin. Lower Cretaceous to present day. Ex. *S. petalifera*, Upper Greensand.

Acrosalenia. Form similar to *Peltastes*. Apical disc rather large; genital plates large, the posterior smaller than the others and differing in shape. A sur-anal, and sometimes other extra plates, in front of the periproct, which is in the antero-posterior line and situated posteriorly. Ambulacral plates compound at and below the ambitus; pores unigeminal except near the peristome. Interambulacra with large perforate tubercles. Spines smooth or striated. Lias to Lower Cretaceous. Ex. *A. spinosa*, Inferior and Great Oolites.

Hemicidaris. Test spheroidal, inferior surface flattened. Apical disc small. Ambulacra narrow on the upper surface, slightly flexuous, with two rows of tubercles which become smaller on the upper surface; plates at and below the ambitus compound, each formed of two to four fused plates; pores unigeminal, but bigeminal near the peristome. Interambulacra broad; plates large and few, each with a large perforate and crenulate tubercle, and also smaller tubercles and granules. Spines cylindrical, long. Peristome large, with well-developed notches. Inferior Oolite to Cretaceous. Ex. *H. intermedia*, Corallian.

Pseudodiadema (fig. 57 A). Test circular or slightly polygonal, sub-hemispherical, depressed. Apical disc and periproct large. Ambulacra straight, narrower than the interambulacra, with two rows of crenulate and perforate tubercles; plates compound, each consisting of three fused primaries, the middle being largest, usually with three pairs of pores on each plate, unigeminal. Interambulacra with two or more rows of primary crenulate and perforate tubercles. Peristome large, decagonal. Lias to Cretaceous. Ex. *P. pseudo-diadema* (= *hemisphericum*), Corallian.

Hemipedina. Test circular or slightly polygonal, depressed. Apical disc rather large. Ambulacra narrow, plates formed of three fused primaries (but simple near the apical disc), pores unigeminal; two rows of tubercles, perforate, not crenulate. Interambulacra with two (sometimes more) vertical rows of primary, perforate, not crenulate tubercles. Spines of moderate length, finely striated. Peristome with slight incisions. Lias to present day. Ex. *H. etheridgei*, Lias.

Diplopodia. Form and tubercles similar to *Pseudodiadema*. Pores bigeminal near the apex and peristome, unigeminal at the

ambitus; plates at the ambitus composed of four primaries or sometimes the lowest plate is a demi-plate. Rhætic to Lower Chalk. Ex. *D. versipora*, Corallian.

Stomechinus (fig. 57 C). Test hemispherical. Genital plates relatively large, projecting outwards; oculars small. Ambulacra wide, plates formed of three primaries—the middle one largest; pores trigeminal. On each ambulacral and interambulacral area are two vertical rows of primary, imperforate, non-crenulate tubercles, of about the same size on each area; also secondary tubercles and granules, usually numerous. Peristome large, with ten deep incisions. Inferior Oolite to Lower Cretaceous. Ex. *S. bigranularis*, Inferior Oolite.

Phymosoma (=*Cyphosoma*) (fig. 57 B). Form similar to *Pseudodiadema*. Ambulacral plates high, compound, each may consist of four, five, or six fused plates (some being demi-plates) with the same number of pairs of pores; two rows of primary imperforate tubercles; pores unigeminal, but bigeminal near the apical disc. Interambulacra with two or more rows of primary imperforate tubercles. Peristome with small notches. Oxfordian to Eocene; common in the Chalk. Ex. *C. koenigi*, Upper Chalk.

Echinus. Test more or less hemispherical. Apical disc as in fig. 55 B. Ambulacra rather narrow, trigeminal, plates compound consisting of a lower primary, a middle demi-plate, and an upper primary or demi-plate. Two vertical rows of small, primary tubercles on each area, and often numerous secondary tubercles. Peristome rather small, circular, with small incisions. Cretaceous to present day. Ex. *E. woodwardi*, Pliocene; *E. esculentus*, Pliocene and living.

ORDER II. IRREGULARIA

The anus is placed outside the apical disc, in the posterior interambulacral area. The mouth is either central or in front of the centre. The test is bilaterally symmetrical. Ambulacra simple or petaloid. Lantern and perignathic girdle may be present or absent.

SUB-ORDER 1. HOLECTYPINA

Peristome central, with notches. Lantern and perignathic girdle present. Ambulacra not petaloid: plates compound or mainly simple.

Galerites (=*Echinoconus*, *Conulus*) (fig. 56 E). Test conical, or almost hemispherical, inferior surface flat, outline pentagonal or oval. Apical disc small, with only four genital plates. Ambulacra narrow, straight, some of the plates compound; pores unigeminal, but trigeminal near the mouth. Interambulacra with broad plates, tubercles very small, perforated and crenulated. Peristome small, central, decagonal. Periproct marginal or submarginal. Upper Greensand to Upper Chalk. Ex. *G. albogalerus* (*conicus*), Upper Chalk.

Holectypus. Test hemispherical, depressed, base excavated. Apical disc small. Ambulacra narrow, straight, some of the plates compound; pores unigeminal, tubercles small. Interambulacra formed of rather large plates, with small tubercles. Peristome central, decagonal, with notches. Periproct large, placed between the peristome and the posterior margin of the test. Upper Lias to Corallian; also foreign Cretaceous. Ex. *H. hemisphericus*, Inferior Oolite.

Discoidea. Form similar to *Holectypus*. On the base of the interior are ten vertical plates extending from the margin of the test towards the mouth, and placed one on each side of the ambulacral areas. Cretaceous. Ex. *D. cylindrica*, Chalk.

Pygaster. Test large, depressed, outline pentagonal or circular, base concave. Apical disc small; madreporic plate large, extending to the front of the periproct. Ambulacra straight, simple; pores unigeminal; tubercles in vertical rows. Interambulacra wide, tubercles perforate. Peristome central, large, decagonal. Periproct very large, placed just behind the apical disc. Lias to Lower Cretaceous. *Pygaster* in a more restricted sense is found in the Middle and Upper Oolites; the Liassic and some Middle Jurassic species are separated under the name *Plesiechinus*; the Cretaceous and some Jurassic species are referred to *Macropygus*. Ex. *P. semisulcatus*, Corallian.

SUB-ORDER 2. CLYPEASTRINA

Peristome central, without notches. Lantern and perignathic girdle present. Ambulacra petaloid, plates simple. Ocular and genital plates fused together.

* **Clypeaster.** Outline sub-pentagonal or ovoid, usually truncated posteriorly; base of test flat, upper surface usually convex in the central part and sloping to the margin often forming a thin edge. Apical disc small. Petaloid parts of ambulacra broad, with the pores widely separated and conjugate. Tubercles small, sunk in depressions; spines very small. Periproct at or near the margin. Peristome central, sunk in a deep depression. Interior with partitions near the edge of the test. Upper Eocene to present day. Ex. *C. grandifolius*, Miocene.

* **Scutella.** Test much flattened, circular or subcircular, broadest posteriorly; base flat, with branching ambulacral furrows radiating from the small central peristome. Apical disc small, central, pentagonal. Ambulacra petaloid, the petaloid parts unequal and nearly closed. Periproct small, infra-marginal. Tubercles very small. Interior of test with supports near the margin. Oligocene and Miocene. Ex. *S. rotunda*, Miocene.

SUB-ORDER 3. SPATANGINA

Peristome excentric, without notches. Lantern and perignathic girdle absent. Ambulacra commonly petaloid, the plates simple; anterior ambulacrum often different from the others. The bilateral symmetry of the test is particularly well-marked.

Hyboclypeus. Test oval, depressed, anterior part usually more elevated. Apical disc elongated—the two anterior genitals separated from the two posterior by two oculars. Ambulacra simple, pores unigeminal. Interambulacra wide. Tubercles very small. Periproct next the apical disc, in a long groove on the dorsal surface. Peristome a little in front of the centre. Inferior Oolite to Corallian Ex. *H. gibberulus*, Inferior Oolite.

Nucleolites (=*Echinobrissus*). Test depressed; outline oval or quadrilateral, rounded anteriorly, truncated and broadest posteriorly; inferior surface concave. Apical disc compact, four perforate genital plates, and one imperforate. Ambulacra sub-petaloid, pores unigeminal, the outer pore elongated in the sub-petaloid part. Interambulacral plates wide, tubercles small. Peristome oval or pentagonal, excentric, a little anterior. Periproct placed in a sulcus on the dorsal surface. Inferior Oolite to present day. Ex. *N. scutatus*, Corallian.

Clypeus. Test large, flattened, more or less discoidal, with circular or pentagonal outline, and flat or concave base. Apical disc small. Ambulacra large, petaloid, pores unigeminal (except near the peristome), outer pore elongated and in a long groove. Peristome nearly central, with a floscelle. Periproct on the dorsal surface, often in a sulcus. Tubercles very small. Inferior Oolite to Corallian. Ex. *C. ploti*, Inferior Oolite.

Catopygus. Test small, oval, elevated, truncated behind, with flat base. Apical disc small. Ambulacra sub-petaloid, unigeminal, outer pore elongated in the sub-petaloid parts. Tubercles very small. Periproct high up on the posterior end. Peristome a little excentric, small, with a floscelle. Cretaceous to present day. Ex. *C. columbarius*, Upper Greensand.

Collyrites (fig. 56 C). Test ovoid, inflated. Apical disc greatly elongated; at the anterior end are four perforated genital plates separated by two oculars, at the posterior end are two oculars; these two groups of plates are connected by numerous small plates. Ambulacra simple, pores unigeminal. The three anterior ambulacra meet at the anterior end of the apical disc, the other two meet at the posterior end. Interambulacra broad, tubercles small. Peristome excentric. Periproct above the posterior margin. Upper Lias to Cretaceous. Ex. *C. bicordata*, Corallian.

Echinocorys (=*Ananchytes*) (fig. 56 B). Test very convex above, inferior surface flattened, outline oval. Apical disc elongated; the four genital plates perforated, the two anterior separated from the two posterior by two large ocular plates. Ambulacra simple, pores unigeminal. Interambulacral plates large, tubercles small. Peristome anterior. Periproct oval, infra-marginal. Upper Chalk. Ex. *E. vulgaris*.

Holaster (fig. 62). Test heart-shaped, inferior surface more or less flattened, superior surface with a broad shallow groove in front. Apical disc elongate, the two pairs of genital plates separated by two oculars. Ambulacra large, simple; pores uni-

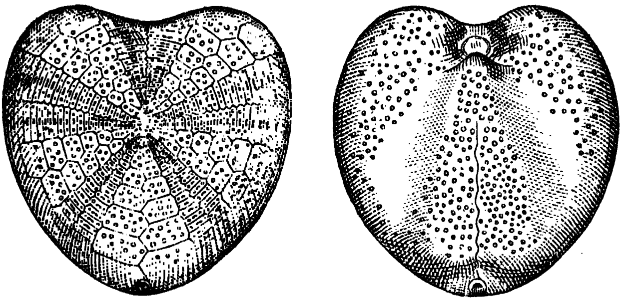


Fig. 62. *Holaster subglobosus*, Chalk. Upper and lower surfaces. $\times \frac{2}{3}$.

geminal, round or elongate; the anterior ambulacrum in the groove. Interambulacra with small tubercles and granules. Peristome near the anterior margin, elliptical. Periproct supra-marginal. Upper Greensand and Chalk; also Tertiary in Australia. Ex. *H. subglobosus*, Lower Chalk.

Cardiaster. Form similar to *Holaster*, but anterior groove usually with sharp borders. Apical disc similar to *Holaster*. Pores elongate, unigeminal. Small perforate and crenulate tubercles. Peristome near the anterior margin, with a projecting lip. Periproct on the posterior truncated end. Fasciole passes beneath the periproct and round the margin of the test. Cretaceous. Ex. *C. ananchytis*, Chalk.

Micraster (figs. 59, 63). Test heart-shaped or oval. Apical disc small, excentric. Ambulacra sub-petaloid, placed in sunken areas, the sub-petaloid parts of the two anterior lateral longer than those of the two posterior lateral; pores unigeminal. The anterior unpaired

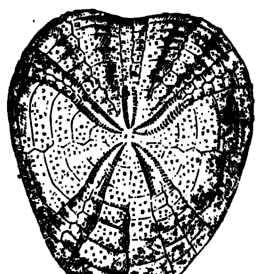


Fig. 63. *Micraster cor-bovis*. Upper Chalk. $\times \frac{1}{2}$.

ambulacrum in a deep groove, with its pores circular. Interambulacra with large plates; tubercles small, perforate and crenulate. Fasciole below the anus. Peristome near the anterior border, with a projecting lip. Periproct on the upper part of the posterior end. On the under surface the posterior interambulacrum bulges out forming a *plastron*. Middle and Upper Chalk; also Tertiary in Australia. Ex. *M. cor-anguinum*, Upper Chalk.

Hemiaster. Form similar to *Micraster*. A peripetalous fasciole only. Cretaceous to present day. Ex. *H. bailyi*, Gault.

Schizaster. Test heart-shaped, highest behind, with excentric apex. Anterior ambulacrum long, placed in a groove; other ambulacra petaloid and in deep grooves—the posterior pair much shorter than the antero-lateral pair. Peristome near the anterior margin, with projecting lip. Periproct on the posterior truncated end of the test. A peripetalous fasciole, and usually also a lateral fasciole diverging from the former and passing beneath the periproct. Eocene to present day. Ex. *S. d'urbani*, Bracklesham Beds.

Distribution of the Echinoidea

Some echinoids live at great depths in the ocean, no less than a dozen species having been found below the 2000 fathom line, and one even at 2900 fathoms; but by far the larger number occur near the coasts in shallow water; thus, of the 297 existing species recorded by Agassiz, 201 are found in water of less than 150 fathoms in depth. Echinoids are most abundant where the sea-bottom is rocky, sandy, or calcareous, and less common where it is muddy; consequently fossil forms are rare in clayey strata. Those found in deep water have a much wider range in space than those found in shallow water. Many genera, especially those with a considerable range in depth, have also a long range in time, some extending back to the Cretaceous or even to the Jurassic period, *e.g.* *Hemipedina, Nucleolites, Catopygus, Salenia, Hemiaster.*

The Palæozoic echinoids, with possibly two exceptions, are regular forms; they are remarkable for possessing more than twenty columns of plates in the corona (except in *Bothriocidaris*), and frequently the plates overlap, rendering the test flexible. Echinoids are rare in Palæozoic formations, especially in those of pre-Carboniferous age. The earliest form is *Bothriocidaris*, from the Ordovician of Russia, which possesses only one column of plates in each interambulacrum; in the Silurian, genera with numerous columns of plates appear, viz. *Echinocystis*, *Palæodiscus* and *Koninckocidaris*; in the Devonian, *Lepidocentrus* occurs; in the Carboniferous, genera with numerous columns of plates reach their maximum development, viz. *Palæechinus*, *Maccoya*, *Melonechinus* (=*Melonites*), *Perischodomus*, *Lepidesthes* and *Archæocidaris*. *Miocidaris*, the earliest representative of the Cidaridæ, appears in the Carboniferous and Permian but is more abundant in the Trias and Lower Jurassic; it is the oldest echinoid known with two columns of plates in each interambulacral area. Cidaridæ are common in the Trias of St Cassian and Bakony, where a few other regular echinoids also occur and show for the first time the presence of branchial incisions in the peristome.

In the Jurassic rocks the echinoids are much more numerous, relatively to the other groups of animals, than in the earlier formations; they are comparatively rare in the Lias and the other clayey divisions, but very abundant in the calcareous beds, especially in the Inferior Oolite and the Corallian. In the Lias the chief forms are *Cidaris*, *Hemipedina*, *Diademopsis*, *Pseudodiadema*, and *Acrosalenia*; irregular echinoids (viz. *Pygaster* (*Plesiechinus*), *Holectypus*, *Galeropygus* and perhaps *Collyrites*) make their first appearance in the Upper Lias. The genera which are best represented in the Middle and Upper Jurassic are, of

the regular group, *Cidaris, Hemicidaris, Acrosalenia, Pseudodiadema, Diplopodia, Hemipedina*, and *Stomechinus*; of the irregular group, *Collyrites, Clypeus, Pygurus, Hyboclypeus, Nucleolites* (= *Echinobrissus*), *Holectypus*, and *Pygaster*.

In the Cretaceous the echinoids are even more abundant than in the Jurassic, and attain their greatest development in the upper division of the system; many of the genera found in the Lower Cretaceous occur also in the Upper Jurassic, but the irregular forms are more numerous than hitherto, and show a still greater development in the Upper Cretaceous. The most important genera are, (1) regular, *Cidaris, Pseudodiadema, Phymosoma* (= *Cyphosoma*), *Peltastes, Salenia*; (2) irregular, *Discoidea, Galerites* (= *Echinoconus*), *Hemiaster, Micraster, Cardiaster, Holaster, Echinocorys* (= *Ananchytes*).

Between the Cretaceous and the Eocene there is, in Britain, a great break in the succession of the echinoids; not a single species is common to the two systems, and most of the genera also are different. This change is due in part to the great difference in the conditions under which the deposits were formed, the Chalk being a comparatively deep-water formation, and the Eocene beds, shallow water; but the Eocene forms differ much more from those of the Upper Chalk than from those of the Chalk Marl, the latter deposit having been formed in water of less depth. Throughout the English Tertiaries the echinoids are much rarer than in the Cretaceous; in the Eocene this can be accounted for largely by the fact that the sea-bottom was for the most part muddy; in the Oligocene by the prevalence of freshwater and estuarine conditions; and in the Pliocene, by the lower temperature of the ocean. The London Clay echinoids belong to tropical or sub-tropical genera. The commonest

forms in the Eocene of England are *Hemiaster* and *Schizaster*. In the Eocene of the South of Europe, India, etc., echinoids are numerous; the regular forms are less important than in earlier formations, but the Clypeastrina and Spatangina, in this and subsequent deposits, become increasingly abundant. The Pliocene echinoids found in East Anglia include some forms similar to those found in the North Atlantic. and others which show considerable affinity to species now living in the West Indian seas; the principal genera represented are *Echinus*, *Echinocyamus*, *Spatangus*, and *Temnechinus*.

CLASS III. HOLOTHUROIDEA

This Class includes the sea-cucumbers. They possess an elongated and usually cylindrical body with the mouth at one end and the anus at the other; around the mouth is a circle of tentacles, which are really modified tube-feet. From the water-vascular ring five radial vessels are given off and end near the anus; branches also go to the tentacles. In *Synapta* and its allies tube-feet (with the exception of the tentacles), as well as radial vessels, are absent. The stone-canal in almost all cases opens into the body-cavity. The integument is leathery, and the skeleton is very poorly developed, consisting of minute isolated pieces of various shapes, such as spicules, anchors, and wheels (fig. 64).


A B C

Fig. 64. A, B, anchor and plate of *Synapta tenera*, Recent. C, wheel of *Chirodota convexa* from the Inferior Oolite. Enlarged.

At the present day the Holothurians are widely distributed, but owing to the nature of their hard parts they are rarely found fossil. Specimens found in the Middle Cambrian of British Columbia are regarded by Walcott as

Holothurians. The earliest known European forms, represented only by skeletal structures, occur in the Carboniferous rocks of Scotland, and in the Permian of Germany; a few specimens have been recorded from Jurassic, Cretaceous and later formations. *Synapta* has been found in the Oligocene.

II. PELMATOZOA

The Pelmatozoa, unlike the Eleutherozoa, are generally sedentary, being attached to the sea-floor or some foreign object by the aboral surface, usually by means of a jointed stem; in most cases the attachment is permanent, but it may be temporary only. The group is essentially distinguished by the ciliated grooves which radiate from the mouth; the cilia produce a current of water which carries small organisms to the upwardly directed mouth. The Classes of the Pelmatozoa are: (1) Crinoidea, (2) Cystidea, (3) Blastoidea, (4) Edrioasteroidea.

CLASS I. CRINOIDEA

The Crinoidea include the sea-lilies and feather-stars. The skeleton consists of a *stem*, a *calyx*, and movable *arms* given off from the margin of the calyx (fig. 65).

The calyx is more or less globular, or cup- or basin-shaped, and contains the digestive and other important organs; the mouth is either at or near the centre of the ventral or oral surface, and the anus, which is excentric and inter-radial, is also on the oral surface, and is usually situated at the end of a tubular process. There is a groove on the ventral surface of each arm, and these grooves—the *food-grooves*—are continued over the oral surface to the mouth; they are lined with cilia, by the movements of which food is conveyed to the mouth. There are generally

five arms, but each may branch repeatedly. Immediately under the groove of each arm there is a radial nerve-cord; these cords unite to form larger trunks and ultimately join as a ring round the mouth. Beneath the nerve of each arm is a radial vessel of the water-vascular system, which is continued over the oral surface and joins a ring round the mouth; from this ring tubes hang down and open into the body-cavity, which communicates with the water of the exterior by means of pores. In connection with the radial vessels are tubular processes, the tentacles, which form a row on each side of the food-grooves, and correspond with the tube-feet of the star-fish, but do not function in locomotion. In addition to the nervous system already mentioned, there is another supplying the aboral elements of the skeleton; from a centre at the aboral pole of the calyx nerve cords are given off, which pass through canals in the plates of the calyx to the arms and pinnules, and also into the stem when present.

The stem (figs. 65, 67, *a*) in the crinoids is more or less flexible, and is sometimes several feet in length. It consists of a number of segments, known as *columnals*, which may be disc-like or pentagonal (occasionally square or elliptical); or they may be higher than broad, forming cylinders; these columnals articulate by their flat surfaces, which are often provided with radiating striæ or with ridges in the form of a rosette. Each columnal is pierced at the centre by a canal which is circular or pentagonal and contains a prolongation of the aboral nervous system and vascular organ. From the stem small branches known as *cirri* are sometimes given off; these have a structure similar to that of the stem, and are also pierced by a central canal. The columnals are generally of different heights—larger plates being separated by smaller; the former are first developed, and the latter

are those which have subsequently developed between them. Cirri are borne on some of the larger columnals. The lower end of the stem may taper, but often expands and branches, forming a root-like structure which serves to fix the animal.

The part of the calyx below the origin of the free arms is called the *dorsal cup* (fig. 65); the part above them is the *tegmen*. The dorsal cup consists at its base of a cycle of five plates, known as *basals* (figs. 66, *b*; 67, *c*); but, owing to fusion, the number of basals is sometimes reduced to four, three, or rarely two. In some forms there is below the basals and alternating with them another row of plates (five or three), termed *infra-basals* (fig. 67, *b*), and the base is then said to be *dicyclic*; when basals only are present, it is *monocyclic*. Above the basals, and alternating with them, is a cycle of five *radial* plates (fig. 66, *r*; fig. 67, *d*), which usually form the sides of the dorsal cup; each radial is in a direct line with one of the arms. In some genera there are, between the two posterior radials, other plates, the *anal inter-radials* (fig. 66, *a*; fig. 67, *e*). Sometimes there are inter-radial plates between the other radials as well.

The arms are characteristic of the Crinoidea; they come off directly from the radials, and are formed either of a single or of a double row of plates, the *brachials*; when there is a single row the arm is termed *uniserial*; when there are two rows it is *biserial*. In biserial arms the plates alternate with one another. The brachial plates are connected by muscles by means of which the movements of the arms are effected. The dorsal or outer surface of the brachial plates is rounded; on the ventral or inner surface there is a groove in which the soft parts, above described, are placed; and there is usually also a perforation below the groove, in which the dorsal nerve-cord is situated.

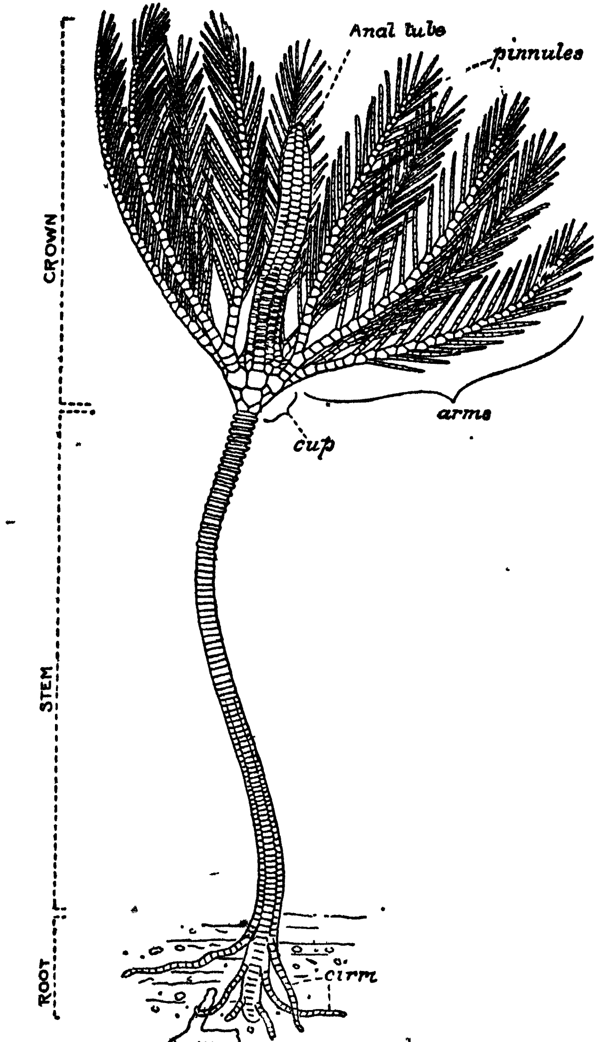


Fig. 65. *Botryocrinus decadactylus*, from the Wenlock Limestone—a simple form of Crinoid, seen from the posterior inter-radius. (From the *Guide to the Geol. Dept., Brit. Mus.*) Natural size.

The groove in the arms is covered over by a series of plates—the *covering plates*, which can be opened and closed, and serve for the protection of the soft parts. Where an arm branches, the brachial which supports two branches (figs. 65, 67, 68 *a*) has sloping sides, and is known as an *axillare*. Small unbranched appendages called *pinnules* occur on the arms of many crinoids (fig. 65); they are similar in structure to the arms, and are given off alternately on opposite sides. In living crinoids the genital products mature in the pinnules. In some forms, the earlier rows of brachial plates become firmly united to one another and to the radials (figs. 66, 70, 2, 3, *br*); these *fixed brachials* have often been regarded as radials, but morphologically they are only brachials which have become incorporated into the calyx. The fixed brachials may be in contact at the sides, or, as in most Palæozoic crinoids, they may be separated by other plates which are termed *inter-brachials* (fig. 66, *ir*). In the posterior inter-radial area (that which leads up to the anus) the inter-brachial plates are often more numerous than in the other areas. When a stem is absent there may be a single plate (the *centrule*) below the infra-basals (*e.g. Marsupites* fig. 69, *c*), or the infra-basals may fuse with a few of the adjacent columnals to form the *centro-dorsal* plate characteristic of the feather-stars (*e.g. Antedon*).

The tegmen or oral surface of the calyx is usually more or less completely covered by calcareous plates. Sometimes five large triangular plates (*orals*) only occur, between which are the food-grooves leading to the mouth; but usually other smaller plates are also present—the food-grooves being usually covered by plates, sometimes called "ambulacrals," and between them occur numerous "inter-ambulacral" plates. In many Palæozoic crinoids (*e.g. Ac-*

tinocrinus) the tegmen consists of a complete vault or dome of stout plates concealing the mouth as well as the food-grooves and their covering plates; commonly this plated tegmen extends upwards around the anal process forming a tube-like covering.

The various plates of the crinoid skeleton are joined together by fibres of connective tissue continuous with those which form the organic basis of the plates. In some cases adjacent plates become fused owing to the deposition of calcareous material between them.

In the genera described below, the basals, radials, and arms are five in number unless otherwise stated.

A. *Monocyclic Crinoids*

Platycrinus. Basals three, unequal. Radials large. Some fixed brachials. One inter-brachial in each area—more in the posterior (anal) area. No inter-radial. Arms bifurcating once to thrice, uniserial at the lower end, biserial above; pinnules long. Tegmen with small plates; anus sub-central, sometimes at the end of a long process. Stem long, section often elliptical. Devonian, but mainly Carboniferous. Ex. *P. lævis*, Carboniferous Limestone.

Eucalyptocrinus (=*Hypanthocrinus*). Calyx deeply concave at the base; at the bottom of the cavity four basals, at the sides five radials; several cycles of fixed brachials, and some inter-brachials. Tegmen elevated, and forming a central anal tube composed of five rows of large plates. Ten vertical partitions spring from the outside of the tegmen, forming compartments in which the ten arms rest. Arms biserial except at the base. Mainly Silurian; one Devonian species. Ex. *E. decorus*, Wenlock Limestone.

Actinocrinus (fig. 66). Calyx pear-shaped, ovoid, or more or less spherical. Basals three, equal, forming a hexagon. Radials generally higher than wide. The first two rows of brachials firmly united. Inter-brachials numerous; and also one (posterior) inter-radial, above which the inter-brachials are more numerous than in the other areas. Tegmen formed of thick, tubercled, hexagonal

plates, produced into a tube with the anus at the end. Arm-branches ten to thirty, biserial. Stem circular, canal pentagonal. Carboniferous. Ex. *A. triacontadactylus*, Carboniferous Limestone.

Amphoracrinus. In essential structure agrees with *Actinocrinus*, but the dorsal cup is low with few inter-brachials. Anal tube short, excentric. Carboniferous. Ex. *A. amphora.*

B. *Dicyclic Crinoids*

* **Cyathocrinus** (fig. 67). Calyx cup-like. Infra-basals small, equal, pentagonal. Basals large, hexagonal (except the posterior, which is heptagonal and supports the square inter-radial plate). Radials shield-shaped. Arms uniserial, very long, bifurcating from five to seven times, without pinnules. Tegmen produced into a long or short anal tube. Stem round, without cirri. Silurian to Carboniferous. Ex. *C. longimanus*, *C. acinotubus*, Silurian.

Crotalocrinus. Dorsal cup similar to that of *Cyathocrinus*. Some fixed brachials present. Arms uniserial, dichotomous, the branches uniting so as to form lamellar expansions or networks; pinnules absent. Tegmen nearly flat, formed of small plates with five large plates at the centre. Anus near the posterior margin. Stem thick, circular; canal pentagonal; root thick, branching. Wenlock Limestone. Ex. *C. rugosus.*

Botryocrinus (fig. 65). Calyx small, cup-shaped. Infra-basals pentagonal; basals hexagonal (except the two posterior, which are pentagonal); radials with the articular surface occupying ½ to ⅔ of the width; two anal inter-radials, one as in *Cyathocrinus*, another below it on the right. Arms divide, giving ten main branches which often bear smaller branches or pinnules. Anal tube large, sometimes coiled, anus near its base. Stem formed of low plates, often in five pieces. Silurian and Devonian. Ex. *B. decadactylus*, Wenlock Limestone.

Poteriocrinus. Calyx with thin plates. Infra-basals equal. Basals high. Three anal inter-radials present. Radials with well-marked concave articular surfaces which do not occupy the entire width of the plates. Anal tube long. Arms long, branching, with pinnules. (Devonian?), Carboniferous. Ex. *P. crassus*, Carboniferous.

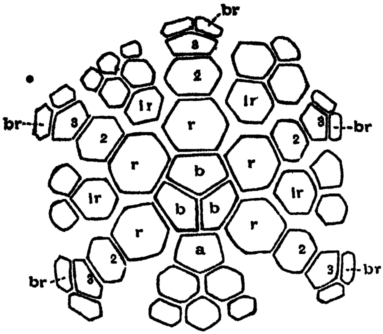


Fig. 66. Diagram of the plates of *Actinocrinus triacontadactylus*, Carboniferous Limestone. *b*, basal plates; *r*, radials; 2, 3, fixed brachials; *br*, brachial plates; *ir*, inter-brachials; *a*, anal inter-radial.

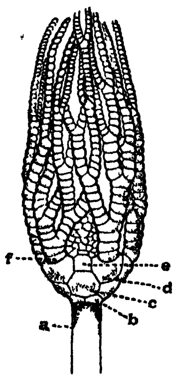


Fig. 67.

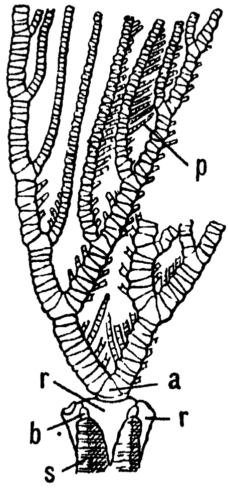


Fig. 68.

Fig. 67. *Cyathocrinus longimanus*, from the Silurian. *a*, portion of stem; *b*, infra-basal plates; *c*, basals; *d*, radials; *e*, anal inter-radial; *f*, first brachial. Reduced.

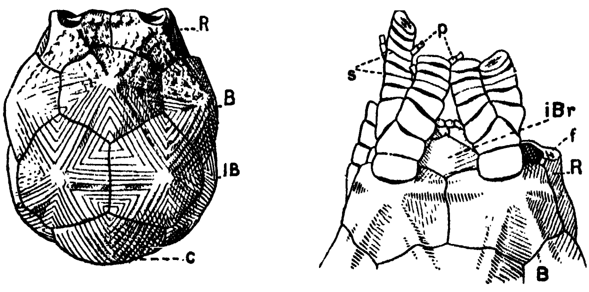
Fig. 68. *Pentacrinus fossilis*, Lias. Calyx and part of stem and arm. (After Bather, 1898.) *s*, stem; *b*, basal plate; *r*, radials; *a*, axillare; *p*, pinnules.

Woodocrinus. Like *Poteriocrinus* but calyx and arms usually shorter; anal tube inconspicuous. The arm-facet occupies the full width of the radial. Carboniferous. Ex. *W. macrodactylus.*

Encrinus. Calyx saucer-shaped. Infra-basals very small, generally concealed by the stem. Basals rather large, hexagonal. Radials large, pentagonal. Two fixed brachials in each ray, the upper being axillary. No inter-brachials, no anal inter-radials. Arms bifurcating, the branches uniserial at first, then alternating, finally biserial; with pinnules. Tegmen covered with plates. Stem long, with small canal. Trias. Ex. *E. liliiformis*, Muschelkalk.

Pentacrinus (fig. 68). Calyx small, bowl-shaped, consisting of small infra-basals, basals, and radials which project like spines over the stem. Arms very long, much branched, uniserial; the small branches all come off on the same side of each main branch. The arms bear pinnules. Stem long, pentagonal, with cirri coming off in whorls; the articular surfaces of the columnals with five raised, crenulate, petaloid parts which are narrow and quite distinct from one another. Jurassic. Ex. *P. fossilis*, Lias.

Marsupites (fig. 69). Calyx large, globular; plates large and thin. Stem absent. Base formed of a large central pentagonal



1. 2.

Fig. 69. *Marsupites testudinarius*, Upper Chalk. (From Bather.) 1. Calyx from the side. 2. Radials and arms. *c*, central plate; *IB*, infra-basals; *B*, basals; *R*, radials; *iBr*, inter-brachial; *f*, fulcral ridge of radial facet; *p*, pinnules; *s*, junction of brachial plates.

plate (*c*). Infra-basals pentagonal. Basals hexagonal. Radials pentagonal, with crescentic depressions for the articulation of the arms. Arms relatively short, bifurcating, uniserial; first brachial much narrower than the radial. Upper Chalk. Ex. *M. testudinarius.*

Ichthyocrinus. Three very small infra-basals; five small basals; five radials; two or three cycles of fixed brachials. Anal inter-radial small, below the right posterior radial. Arms in contact all round, interlocking, uniserial; no pinnules. Silurian. Ex. *I. piriformis.*

Sagenocrinus. Infra-basals small. Anal inter-radial sunk between basals; radials large. Numerous cycles of fixed brachials, separated by very numerous inter-brachials. Arms dividing, uniserial; no pinnules. Silurian. Ex. *S. expansus.*

* **Apiocrinus** (fig. 70). Calyx large. Infra-basals enclosed by, and often fused with, the thick basals. Radials low, excavated on their upper surfaces. Four cycles of fixed brachials. Arms ten, bifurcating once or twice, uniserial. Stem long, cylindrical, base expanded; the articular surfaces of the columnals radiately striated. The upper columnals are in contact at the periphery only. The upper part of the stem expands and passes gradually into the calyx; the upper surface of the last columnal is provided with five radiating ridges between which the basals lie. Jurassic, (Lower Cretaceous?). Ex. *A. parkinsoni*, Bradford Clay.

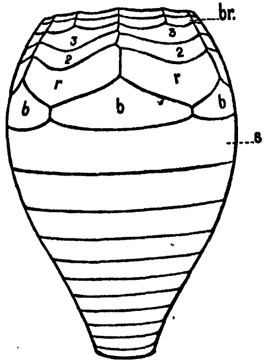


Fig. 70. *Apiocrinus parkinsoni*, from the Bradford Clay. *s*, top columnal of the stem; *b*, basal plates; *r*, radial plates; 2, 3, and *br*, fixed brachial plates. ×⅔.

Millericrinus. Allied to *Apiocrinus.* Usually the top columnal only is widened. Articular facets of radials and brachials well developed. Lias (? also Trias) to Lower Cretaceous. Ex. *M. pratti*, Inferior and Great Oolite.

Bourgueticrinus. Calyx small, with vertical or inwardly-sloping sides; basals about half the height of radials; two rows of fixed brachials; no inter-brachials. Free arms unknown. Stem long, the top columnal very large, as wide as the calyx; upper columnals with circular, others with elliptical articular faces and a transverse ridge across the longer diameter. Cretaceous. Ex. *B. ellipticus*, Chalk.

Distribution of the Crinoidea

Although not so numerous and varied as in the Palæozoic period, the Crinoidea are represented at the present day by a large number of species belonging to about 100 genera. The unstalked forms are the most important (the Antedonidæ, Actinometridæ etc.); these are widely distributed, and occur chiefly in shallow water, but some are found at considerable depths—*Antedon* extending from the shore-line down to 2900 fathoms, and *Actinometra* down to 800 fathoms. The stalked crinoids (*e.g. Isocrinus, Rhizocrinus*) are much less abundant than the unstalked forms, and are found mainly at great depths. In most cases the species of crinoids have only a limited distribution in space.

In the Palæozoic formations the crinoids are much more numerous than the other Echinoderms, their remains (chiefly stems) forming the main part of some limestone beds (crinoidal limestone or marble), as for instance in the Carboniferous. The other Echinoderms are seldom sufficiently numerous to be of importance as rock-builders. The majority of fossil crinoids are stalked forms, and appear to have lived in fairly shallow water, since they are found in association with reef-building corals and other shallow-water organisms.

Crinoids occur first in the Tremadoc Beds. In the Ordovician, *Glyptocrinus, Dendrocrinus*, and a few others have been found. In the Silurian, crinoids become very much more abundant, and attain their maximum development; the most important genera are *Botryocrinus, Calceocrinus, Crotalocrinus, Eucalyptocrinus, Gissocrinus, Ichthyocrinus, Marsipocrinus, Periechocrinus, Pisocrinus, Sagenocrinus, Taxocrinus*. In the Devonian, *Cyathocrinus, Cupressocrinus, Haplocrinus, Hexacrinus* and others are common; in the

Carboniferous, *Actinocrinus, Amphoracrinus, Poteriocrinus, Platycrinus, Rhodocrinus,* and *Woodocrinus.* Crinoids are rare in the Permian. Throughout the Mesozoic formations they are much less abundant than in the Palæozoic; in the Trias the characteristic form is *Encrinus.* In the Jurassic, *Antedon, Isocrinus, Pentacrinus, Saccocoma, Apiocrinus,* and *Millericrinus* are found, the first two living on to the present day. The Cretaceous is characterised by *Bourgueticrinus* and the free-swimming *Marsupites* and *Uintacrinus*—the last two being confined to the Upper Chalk. In the Cainozoic, crinoids are very rare.

CLASS II. CYSTIDEA

The stem in the Cystideans is short, and in some cases absent. The calyx is usually more or less spherical or ovoid, and varies considerably in structure in different types; frequently the plates are very numerous, without radial symmetry, and perforated by numerous canals; food-grooves usually extend from the mouth over the surface of the calyx, and bear simple arm-like structures, called *brachioles* (fig. 72).

In *Glyptosphæra* (fig. 71 A), from the Ordovician, the calyx is spherical, and composed of a very large number of polygonal plates, which are without any radial arrangement such as occurs in the Crinoids and Blastoids. The mouth is at the summit of the calyx, and is covered by five oral plates (*a*), between which the five food-grooves start and extend in a radial manner over the upper part of the calyx, sometimes giving off branches (*b*); at the ends of these grooves are facets (*c*) to which the brachioles were articulated. The grooves were protected by small covering-plates. On one side of the calyx is the anus (*d*), which in perfect

specimens is covered by a pyramid of small triangular plates. Between the mouth and the anus is the madreporite (*e*), which is the external opening of the water-vascular system; just below it is the small, circular genital aperture. All the plates of the calyx are pierced by canals running perpendicularly to the surface; the canals are in pairs, and the external openings of each pair are enclosed in a raised or depressed area of oval shape (fig. 71 B).

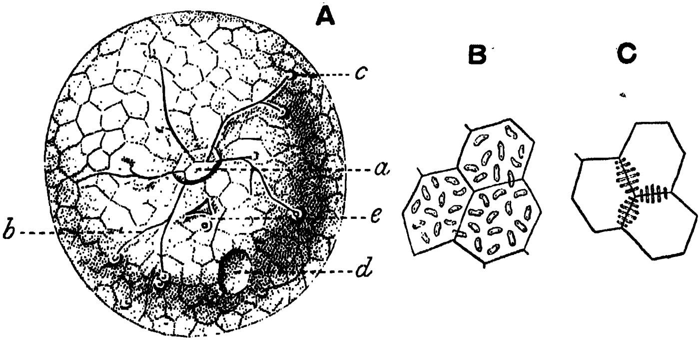


Fig. 71. A. *Glyptosphæra leuchtenbergi*, from the Ordovician of Russia. *a*, mouth covered by oral plates; *b*, food-grooves; *c*, facet for the brachiole; *d*, anus; *e*, just above this is the triangular madreporite, just below is the circular genital aperture (after Volborth). B. A few plates of the same enlarged, showing the pairs of pores. C. Plates of *Echinosphæra*, with pore-rhombs, enlarged.

Some Cystideans are more primitive in character than the form just described. For example, *Aristocystis* from the Ordovician of Bohemia, has an ovoid or pear-shaped body formed of numerous plates, but possesses no food-grooves, brachioles, or stem, and the pores traversing the plates are single.

In another group of the Cystidea the plates of the calyx are traversed by canals which are arranged in groups having a rhombic form; one half of each rhomb is on one plate, the other on an adjoining plate (fig. 71 C). The canals are

parallel to the surface of the plates, and perpendicular to the sutures between the plates. These groups of canals are known as *pore-rhombs*. *Echinosphæra*, from the Ordovician, is a form which possesses many pore-rhombs; it has a spherical calyx, consisting of numerous plates, some of which project at the base and probably served to fix the calyx, there being no stem; around the mouth are from three to five small arms. In most genera belonging to this group the plates of the calyx are much fewer in number than in *Echinosphæra*, and have a distinctly radial symmetry—being arranged in cycles, the plates of each cycle alternating with those immediately below; for example, the calyx of *Lepadocrinus*, from the Silurian (fig. 72), is formed of five cycles of plates; at the base is a cycle of four plates, followed by four cycles of five plates each; from the summit of the ovoid calyx four food-grooves stretch toward the base; they do not rest directly on the calyx, as is the case in *Glyptosphæra*, but on specially-developed plates. Numerous brachioles come off from each side of the food-grooves. In this genus there are only three rhombs, and they are of the more highly-

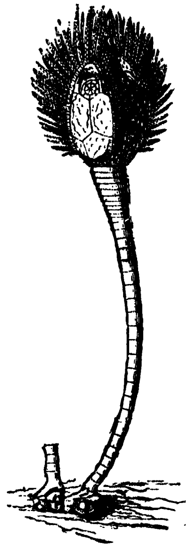


Fig. 72. *Lepadocrinus quadrifasciatus*, from the Wenlock Limestone. Restored figure. The brachioles of the outer rows are erect; those of the middle row depressed. Near the top of the left hand quarter is the anus; near the top of the right-hand quarter is a pectini-rhomb. (From the *Guide to the Geol. Dept., Brit. Mus.*) Natural size.

developed type called *pectini-rhombs,* which differ from pore-rhombs in being surrounded by a raised rim and in having the folds of the plate more pronounced. In some other Cystideans of this group the brachioles are found near the mouth only.

Distribution of the Cystidea

The Cystideans are comparatively rare fossils. They range from the Middle Cambrian to the Devonian, and attain their maximum development in the Upper Ordovician. In the Menevian, *Protocystis* is found; this also occurs in the Tremadoc Beds, and with it *Macrocystella.* In the Ordovician, *Aristocystis, Echinosphæra, Pleurocystis, Glyptosphæra* and others are present; in the Silurian, *Lepadocrinus, Pseudocrinus,* and *Placocystis.* In the Devonian there are fewer forms (*Pseudocrinus, Jackelocystis*).

CLASS III. BLASTOIDEA

In the Blastoids (fig. 73) the body consists of a calyx, usually with a stem; but the latter is rarely found attached to the calyx. The calyx may be spherical, oval, pear-shaped, or bud-like; in most cases it is formed almost entirely of thirteen plates, arranged in a regular manner. True arms are not present.

Pentremites is the commonest Blastoid, and may therefore conveniently be taken as an example of the group. Its calyx (fig. 74) has the following structure. The aboral part is formed of a cycle of three plates—the *basals* (*b*), two of which are alike, and the third smaller. Above the basals is a cycle of five *radial plates* (*r*); these are larger than the basals, and form the main part of the calyx. At

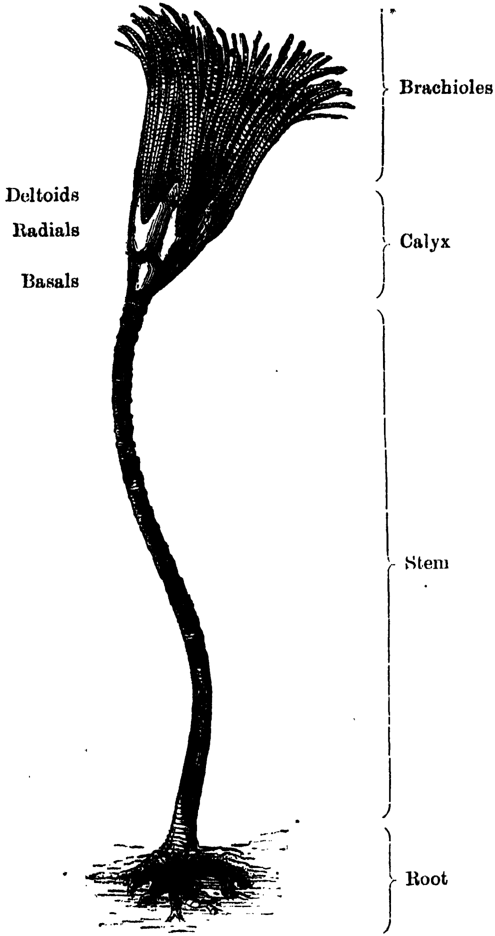


Fig. 73. *Orophocrinus fusiformis*, from the Carboniferous of Iowa. Restored figure. (From the *Guide to the Geol. Dept., Brit. Mus.*) Natural size.

the upper end of each there is a deep incision, which serves for the reception of the food-carrying area (*a*); this is usually spoken of as an "ambulacrum," but there is no evidence of the existence of a radial water vessel, and it is doubtful whether this area is really homologous with the ambulacrum of an Echinoid. Above the radials and alternating with them occur five smaller plates—the *deltoids* (*d*) or inter-radials. The mouth is placed at the summit of the calyx, in the centre, and around it are five other openings termed *spiracles* (*s*), one of which is larger than the others

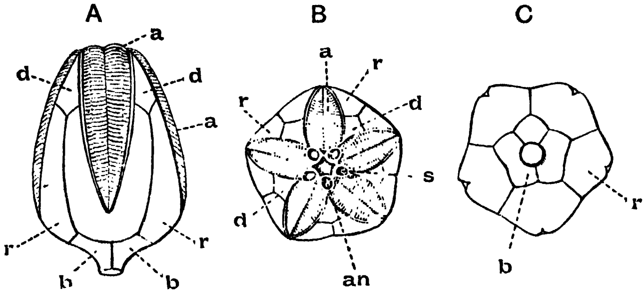


Fig. 74. *Pentremites godoni*, Carboniferous. A, side; B, upper surface; C, under surface. *a*, ambulacra; *b*, basal plates; *r*, radials; *d*, deltoids; *s*, spiracles around the mouth; *an*, anus. × 2

and includes the anus (*an*). From the mouth the five ambulacra (*a*) radiate towards the aboral surface, and are bordered partly by the deltoids but mainly by the radials. Each ambulacrum (fig. 75) consists of the following plates: in the middle is a long pointed plate (*l*), the *lancet-plate*, which is traversed by a longitudinal canal, in which a nerve may have been present. On each side of the lancet-plate is a row of small plates, the *side-plates* (*s*). Extending down the middle of each ambulacrum is the food-groove (*a*), which, in perfect specimens, is covered over by small plates. At right angles to this groove, on each side of

it, are numerous transverse grooves. Along the outer margin of the side-plates there is a row of pores, the *marginal pores* (*p*), formed by spaces between adjoining plates. Beneath each ambulacrum are two *hydrospires* (fig. 76, *h*), one on each side. The hydrospire (fig. 77) is a flattened and folded organ, communicating with the exterior by means of the marginal pores, and also by the spiracles on the oral surface of the calyx. A current of water probably passed in through the former openings and out by the latter. In well-preserved specimens the mouth, as in many crinoids,

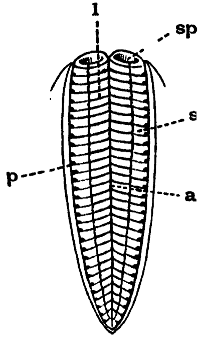


Fig. 75. Ambulacrum of *Pentremites godoni*, Carboniferous. *l*, lancet-plate; *s*, side-plate; *p*, pore; *a*, food-groove; *sp*. spiracle. × 3.

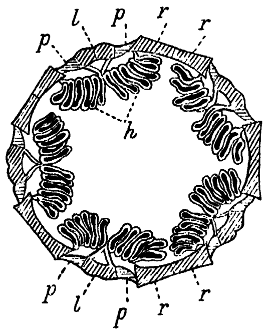


Fig. 76.

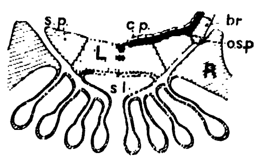


Fig. 77.

Fig. 76. ***Pentremites sulcatus*, Carboniferous. Horizontal section of the calyx. *l*, lancet-plate; *p*, side-plates; *r*, radial plates; *h*, hydrospires (not quite correctly drawn, see fig. 77). (After Zittel.) Enlarged.**

Fig. 77. ***Pentremites*, Carboniferous. Section across ambulacrum. *br*, brachiole; *cp*, covering-plates; *L*, lancet-plate; *osp*, outer side-plate; *R*, radial; *sl*, sub-lancet-plate; *sp*, side-plate. (After Bather.) × 5.**

is not visible externally, but is covered over by a roof of small plates. From the margins of the ambulacra pinnule-like appendages known as *brachioles* (fig. 73) are given off; these are seldom preserved, but pits or facets to which they were attached are seen on the side-plates.

The hydrospires are really folded parts of the radial and deltoid plates—the folds being parallel to the margin of the ambulacra. This is seen clearly in *Codaster*, which is a more primitive form than *Pentremites*; in that genus (fig. 78) the folds open directly to the exterior by slits, owing to the fact that they are not covered by the lancet-plate and side-plates; and on account of this circumstance

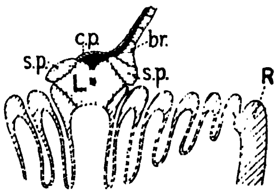


Fig. 78.

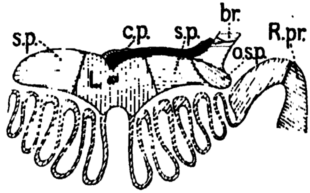


Fig. 79.

Fig. 78. *Codaster trilobatus*, Carboniferous. Section across ambulacrum. (After Bather.) × 5.

Fig. 79. *Phænoschisma verneuili*, Carboniferous. Section across ambulacrum. (After Bather.) Enlarged.

br, brachiole; *cp*, covering-plate; *L*, lancet-plate; *osp*, outer side-plate; *R*, radial; *Rpr*, part of radial; *sp*, side-plate.

spiracles are not developed. In some genera, in which the folds are concealed (fig. 79), the space below the lancet-plate and side-plates, into which the folds open, communicates with the exterior at the oral end by slits or incipient spiracles. A further modification is seen in *Pentremites* (fig. 77) in which, owing to the hydrospire being pushed further into the cavity of the calyx, the folds open into a common canal instead of into the space between the summits of the folds and the overlying lancet-plate and side-

plates; this canal opens orally by true spiracles (fig. 74 B, *s*). The number of folds in each hydrospire varies from one to nine. In a few primitive types hydrospires are absent. In many Blastoids there are five pairs of spiracles and an independent anus, but in some genera (*e.g. Pentremites*) the pairs are confluent so that only five spiracles are present, of which the posterior encloses the anus.

The ambulacra vary in width and length; they may be broad and petaloid or narrow and linear. In some genera the alternate side-plates become squeezed towards the outside of the ambulacrum; here they form an outer row, known as the *outer side-plates*, and are smaller than the plates of the inner row. The side-plates may be entirely at the sides of the lancet-plate (fig. 79), or they may rest on it and partly, or even completely, conceal it (fig. 78). The basals, radials, and deltoids vary considerably in relative size—thus the deltoids may be very small (as in *Troostocrinus*), or they may form a considerable part of the calyx (as in *Orbitremites*).

The most important characters of the Blastoidea as a Class are found in the ambulacra and hydrospires, the absence of true arms, the monocyclic base consisting of three basals only, and the five incised radials. In a few rare cases, hydrospires have been found to be present in the Crinoidea (*Carabocrinus*, *Hybocrinus*).

Codaster. Calyx in the form of an inverted cone or pyramid. Basals forming a conical and usually deep cup; radials large, with the forked parts sharply bent, forming part of the flattened upper surface of the calyx; deltoids and ambulacra confined to upper surface. A long lancet-plate, with side-plates, occurs between the deltoids and radials. Hydrospires consist of sharp folds of the calyx where the radials and deltoids meet, and open at the surface by slits. Mouth pentagonal, originally plated over; no spiracles; anus between the posterior deltoid and radials. Silurian to Carboniferous. Ex. *C. trilobatus*, Carboniferous.

Orbitremites (= *Granatocrinus*). Calyx elliptical, ovate, or more or less spherical, in section pentagonal or round; with concave base. Basals small, not seen in a side view. Radials of variable size and forming part of the base. Deltoids generally rhombic, large in some species, small in others. Ambulacra narrow, straight, with nearly parallel sides. Lancet-plate narrow. Hydrospires simple, usually with two or three folds only, dilated at the free ends; the inner fold forms a plate next to the lancet-plate. Spiracles five, round or oval, piercing the apices of the deltoids, the posterior one including the anus. Carboniferous Limestone. Ex. *O. derbiensis*.

Distribution of the Blastoidea

In England the Blastoids range from the Devonian to the Carboniferous, being most abundant in the latter. A few primitive types (*Asteroblastus*, *Blastoidocrinus*) occur in the Ordovician of Russia and Canada; and some others (*Troostocrinus*, *Codaster*) are found in the Silurian of North America. The English Devonian forms are rare and but little known. In the Carboniferous Limestone the blastoids attain their maximum development; ten genera are represented, the most important being *Codaster*, *Orophocrinus*, *Schizoblastus*, *Orbitremites* and *Mesoblastus*. *Pentremites* is common in the Carboniferous of America, but is not found in Britain. A number of genera have been found in the Permian of Timor.

CLASS IV. EDRIOASTEROIDEA

The calyx in the Edrioasteroids (fig. 80 A) is usually composed of a large number of irregular plates, and in most cases is flattened and more or less circular in outline; it is attached to some foreign body by the under part—a stem being rarely if ever present. The mouth is at the centre of the upper surface (*ps*), and is covered by plates; from it five ambulacra extend outwards over the upper

surface of the calyx, and sometimes over part of the lower surface also. The ambulacra do not branch as a rule, but are frequently curved. The ambulacral grooves are covered by two rows of alternating plates (*amb*), similar to the covering-plates of crinoids. In *Edrioaster* and its near allies the floor of each groove is formed of special plates (*ad*), between or at the outer margins of which are pores (*p*) which may indicate the existence of tube-feet. Neither brachioles nor arms are developed in connexion with the

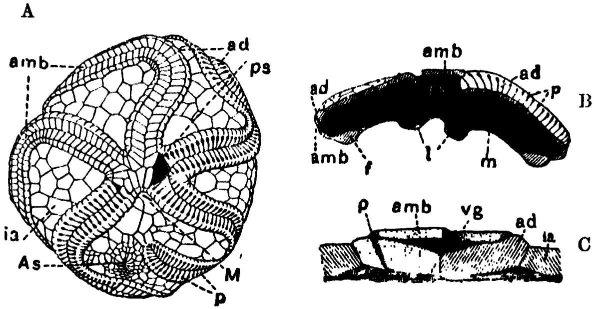


Fig. 80. *Edrioaster bigsbyi*, Ordovician of Canada. (From Bather.)

A. Oral surface. *amb*, covering-plates over the anterior and left-anterior ambulacral grooves, but removed from the other grooves; *ad*, floor-plates of ambulacral grooves; *p*, pores between floor-plates; *ps*, peristome, the greater part of which is roofed by enlarged covering-plates; *ia*, interambulacrum; *M*, madreporite; *As*, anus. Natural size.

B. Section across the same specimen through the right anterior ambulacrum and the left posterior interambulacrum. Lettering as in A. *f*, frame of stouter plates; *m*, membrane with overlapping plates thrown into five lobes (*l*). Natural size.

C. Section across an ambulacrum with covering-plates (*amb*) over the groove (*vg*). Enlarged.

ambulacra. The anus, which is covered by a pyramid of plates, is on the upper surface—in the area between the two posterior ambulacra (*As*). The calyx was more or less flexible in some cases; and frequently around its border on the upper surface (but sometimes on the lower, fig. 80

B, *f*) there is a series of larger marginal plates, forming a framework, which, in combination with the five conspicuous ambulacra, gives the upper surface something of the appearance of a star-fish in which the rays are not prolonged.

The Edrioasteroids include only a few genera, and have usually been regarded as Cystidea, but differ in the absence of brachioles, and in the occurrence of pores between the flooring-plates, suggestive of the presence of a radial water vessel with tube-feet.

Distribution of the Edrioasteroidea

The Class ranges from the Cambrian to the Carboniferous, and is best represented in the Ordovician. The principal genera are:—*Stromatocystis* in the Cambrian; *Cyathocystis, Edrioaster* and *Steganoblastus* (?) in the Ordovician; *Pyrgocystis* in the Silurian; and *Agelacrinus* and *Lepidodiscus*, ranging from the Ordovician to the Carboniferous.

PHYLUM ANNELIDA

CLASS CHÆTOPODA

THE Chætopoda include various forms of worms. The body is segmented and generally the segments are numerous and similar. There is a ventral nerve-cord with ganglia, and a nerve-ring round the œsophagus connected with a pair of ganglia above it. A vascular system and a body-cavity (cœlom) are present. The cuticle is thin and flexible. The majority of the Chætopoda possess bristle-like processes termed setæ or chetæ which assist in locomotion. There are four orders, (1) the Archiannelida, *e.g. Polygordius*; (2) the Oligochæta, *e.g.* the common earthworm *Lumbricus*; (3) the Polychæta; (4) the Hirudinea or leeches. Only the Oligochæta are definitely known as fossils.

ORDER III. POLYCHÆTA

The members of this Order are nearly all marine, and are characterised by the possession of numerous setæ arranged in bundles on each segment; the setæ are usually placed on lobes or flaps on the sides of the segments termed *parapodia.* Tentacles are usually present on the head. Many forms live in tubes, which may consist of carbonate of lime, of chitinous material, or of grains of sand cemented together by a secretion; the tubes are sometimes free, but often attached to some foreign object. On account of the

possession of this tube the polychætous worms are often found fossil. Other forms, which do not live in tubes, are provided with minute chitinous jaws, and in some formations, especially the Ordovician and Silurian, these are abundantly preserved.

Serpula. Tube calcareous, long, round, angular or flattened; straight, curved irregularly or sometimes spirally, closed at one end; generally attached to some foreign object by a portion of its surface. Silurian to present day. Ex. *S. gordialis*, Chalk.

Spirorbis. Tube calcareous, small, spiral, attached by one side. The spiral either left-handed or right-handed, the last whorl often produced into a free tube. Ordovician to present day. Ex. *S. pusillus* (= *carbonarius*), Carboniferous.

Distribution of the Chætopoda

Nearly all the worms which are found fossil belong to the Order Polychæta; the earliest examples occur in the Cambrian Beds. In addition to worm-tubes and jaws, there are, in various rocks, numerous trails and burrows, which are considered by some authors to have been formed by worms, but in many cases it is probable that they were made by other animals such as crustaceans and gasteropods.

PHYLUM BRACHIOPODA

Classes.		*Orders.*
1.	Inarticulata	1. Atremata.
		2. Neotremata.
2.	Articulata..............	1. Protremata.
		2. Telotremata.

IN the Brachiopods the soft parts of the animal are enclosed in a shell which is formed of two parts termed *valves*, one placed on the dorsal surface, the other on the ventral. Generally the main part of the body occupies only the posterior portion of the shell. The interior of the shell is lined by the body-wall, and by the *mantle*, which is a prolongation of the body-wall and is divided into two lobes, one occurring in each valve; the space between the two is known as the *mantle-cavity*. The shell is secreted by the mantle. In most genera the margin of the mantle is thickened. and carries numerous chitinous setæ. The mouth (fig. 81, *v*) opens into the mantle-cavity, and leads into an œsophagus, which is followed by a stomach (partly surrounded by the liver), and an intestine. In the articulate brachiopods the intestine is short and ends blindly, in the inarticulate forms it is long and ends in an anus which opens into the mantle-cavity. The nervous system consists of a ring round the œsophagus, with ganglionic enlargements from which nerves are given off to the arms, mantle, etc. The part of the body-cavity which

surrounds the alimentary canal communicates with the mantle-cavity by means of two, or rarely four, funnel-shaped canals, which serve as excretory organs. The body-cavity extends into the mantle as a series of spaces or sinuses; these produce slight depressions on the interior of the valves, and can often be traced as ridges on the internal casts of fossil specimens (fig. 98). The body-cavity is filled with a fluid which is kept in motion by means of cilia. The heart is on the dorsal surface of the stomach.

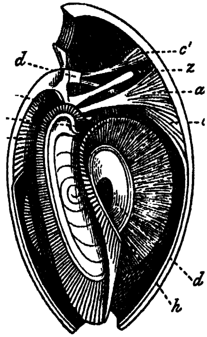


Fig. 81. *Magellania* [= *Waldheimia*] *flavescens*, Recent. Longitudinal section. *d*, (upper), cardinal process; *d*, (lower), arms; *h*, cirri (tentacles); *a*, adductor muscles; *c*, *c'*, divaricator muscles; *ss*, septum; *v*, mouth; *z*, terminal part of alimentary canal. (After Davidson.) × 1½.

The brachiopods are never colonial animals. Reproduction takes place sexually, and the sexes are usually separate. The genital organs are placed in the body-cavity, and in the sinuses of the mantle.

Generally the greater part of the mantle-cavity is occupied by two long processes, given off from the sides of the mouth; these are known as the "*arms*" (fig. 81, *d*), since they were at first supposed to serve in locomotion—hence the name *Brachiopoda*. The arms are covered with cirri (or tentacles) (*h*), the cilia on which produce a current of water conveying food to the mouth. Respiration is carried on mainly by the mantle, but possibly also to some extent by the arms.

Of the two valves of the brachiopod, the ventral is nearly always larger than the dorsal; each is produced

into a beak or *umbo* (fig. 82). The ventral umbo is more prominent than the dorsal, and has generally, either at its apex or just beneath it, an opening. With a very few exceptions the shell of the brachiopod is equilateral, that is to say, a line drawn from the umbo to the opposite margin divides it into two equal and similar parts. This character, combined with the inequality in the size of the valves and the perforation at the umbo, renders it easy to distinguish the shell of a brachiopod from that of a lamellibranch. In many forms the two valves are joined together by means of a hinge, these constitute the group *Articulata*; in others they are held together by the muscles

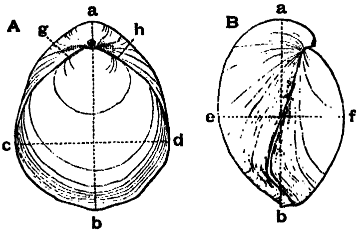


Fig. 82. *Terebratula semiglobosa*, Upper Chalk. A. Dorsal view. B. Lateral view. *a*, posterior; *b*, anterior; *a—b*, length; *c—d*, breadth; *e—f*, thickness; *g—h*, hinge-line. × ⅘.

and the mantle only, these form the *Inarticulata*. The hinge consists of two short curved processes or teeth given off from the ventral valve near the umbo, which fit into corresponding sockets in the dorsal valve. In some genera (*e.g. Orthis*) the teeth are supported by plates (the *dental plates*) which are fixed to the inside of the ventral valve. The part of the margin of the valves where the teeth occur and on which the two valves move in the opening and closing of the shell, is termed the *hinge-line* (fig. 82, *g—h*). In some genera (*Terebratula*) this is short and curved, in others (*Spirifer*, fig. 95) it is long and straight. The

posterior part of the shell is that near the hinge (fig. 82, *a*), the anterior is the opposite margin (*b*). The length of the shell is measured from the anterior to the posterior border (*b*—*a*). The breadth is at right angles to this, from one side of the shell to the other (*c*—*d*). The thickness is measured from one valve to the other, perpendicular to the length and breadth (*e*—*f*). In some genera (*e.g. Terebratula*) the length is greater than the breadth, in others (*e.g. Strophomena*) the breadth is greater. Between the hinge-line and the umbo there is in some brachiopods (*e.g. Cyrtia*, fig. 83) a flat or slightly concave portion of the shell, usually triangular, on which the ornamentation of the rest of the shell is absent, the surface being either smooth or striated; this is known as the area. It may occur on both valves (*e.g. Orthis*), but is sometimes found on the ventral valve only.

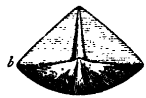


Fig. 83. *Cyrtia exporrecta*, Wenlock Limestone. *a*, umbo of ventral value; *abc*, area with deltidium in the middle; *b*—*c*, hinge-line. Natural size.

Nearly all living brachiopods are fixed to a rock or other object; but some fossil forms were free, especially in old age (*e.g. Productus*). Some, like *Crania*, are attached by the close adhesion of one valve to the rock; others (*e.g. Strophalosia*) by spines given off from the surface of the shell. More commonly, however, the attachment takes place by means of a stalk or peduncle; this is a cylindrical process, in some genera long, in others short, connected with the mantle, and passing out either through an opening in the ventral valve (fig. 84 A, *f*) or between the umbones (*e.g. Lingula*, fig. 88). It is composed mainly of supporting-tissue with a sheath of horny material, but in some forms there are muscular layers also. In *Lingula*, which commonly lives in burrows in the sand of the sea-floor, the

contraction of the muscles of the peduncle serves to withdraw the animal from the surface into its burrow.

The opening for the passage of the peduncle varies considerably in different genera, and is a feature of importance in classification. The simplest case is that found in *Lingula* and other similar forms, in which the opening is shared by both valves. In other types we find that the peduncle-opening is confined to the ventral valve; in *Discina* the opening is completely enclosed by the shell and is often near the centre of the valve, consequently the peduncle comes out at right angles to the plane of the valves. Sometimes, as in *Orthis* (fig. 93), the peduncle-opening is in the form of a triangular fissure, under the umbo, known as the *delthyrium*. In brachiopods belonging to the group Telotremata, a delthyrium is found in young individuals, but subsequently becomes partly closed by two plates, which grow inwards from the sides of the delthyrium and sometimes meet in the middle line. These two plates form the *deltidium* (fig. 84 A, *d*). In *Rhynchonella* the two plates usually meet, but a small circular or ovate opening (the *foramen*) is left near the centre for the peduncle. In *Magellania* (fig. 84 A, *f*) the foramen is quite at the apex of the umbo, its lower boundary being formed by the deltidium (*d*). In genera belonging to the Protremata and a few of the Neotremata, the delthyrium is more or less completely closed by a single plate known as the *pseudo-deltidium*; this at first sight closely resembles the deltidium, but is really of a different nature. It originates on the dorsal surface of the body, but subsequently becomes attached to the ventral valve, and then continues to grow by secretion from the peduncle. The deltidium, on the other hand, is formed by the edge of the ventral lobe of the mantle and consists of a pair of plates

which, in some cases, coalesce. The pseudo-deltidium is developed at an earlier stage in the life of the individual than the deltidium, and grows from the apex of the delthyrium downwards, becoming fused to the ventral valve.

The two valves of the brachiopod can be opened and closed by means of muscles (fig. 81); those which open them are called the *divaricators* (*c*, *c′*), those which close them, the *adductors* (*a*). When the soft parts of the animal have been removed the places where the muscles were attached

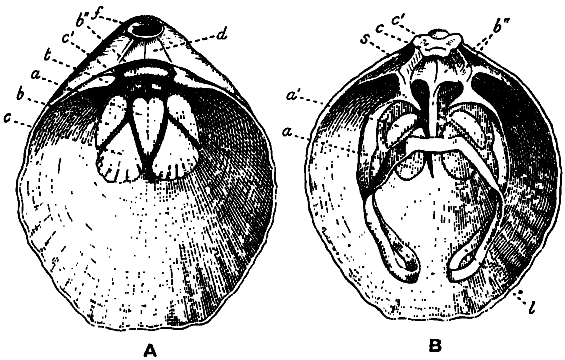


Fig. 84. *Magellania* [= *Waldheimia*] *flavescens*, Recent. A. Interior of ventral (or pedicle) valve. *f*, foramen; *d*, deltidium; *t*, teeth; *a*, impressions of adductor muscles; *c*, *c′*, impressions of divaricator muscles; *b*, *b″*, muscles of the peduncle. B. Interior of dorsal (or brachial) valve. *c*, *c′*, cardinal process; *b″*, hinge-plate; *s*, dental sockets; *l*, loop; *a*, *a′*, adductor impressions; *c*, point of attachment of the smaller divaricator. (After Davidson.) × 1½.

to the interior of the shell are indicated by a difference in the surface such as striation, or by slight depressions or elevations; these markings are termed the *muscular impressions* (fig. 84). In the articulate brachiopods there are generally five or six pairs of muscles. In the genus *Magellania* there are two pairs of divaricators (fig. 81 *c*, *c′*) and one of adductors (*a*). Both pairs of the former are attached

to a process (the *cardinal process*, fig. 84 B, *c*, *c′*) on the dorsal valve between the teeth sockets, and one pair join the ventral valve near its centre (fig. 84 A, *c*), while the other pair, which are smaller, are attached nearer the posterior border (*c′*). Hence the dorsal valve forms with these two pairs of muscles a lever of the first order. The adductor muscles are united to the ventral valve near the centre (fig. 84 A, *a*) and form a single impression divided by a median line; these muscles bifurcate before reaching the dorsal valve and there form four impressions (fig. 84 B, *a*, *a′*). There are also muscles attached to the peduncle which serve to move the shell bodily, one pair of these being united to the dorsal valve (fig. 84 B, *b″*), the others to the ventral (A, *b*, *b″*). In the Inarticulata the muscles are usually more complicated; thus, in *Lingula* (fig. 88) we find, in addition to the adductors and divaricators, muscles for moving one valve backward or forward in relation to the other, and others for giving a slight rotary motion.

The arms, already mentioned as occupying in most genera the main part of the mantle-cavity, are generally coiled up. In some forms they can be protruded a greater or shorter distance. Sometimes they are supported on a calcareous framework—the *brachial skeleton*—which is attached to the posterior part of the dorsal valve at the sides of the cardinal process. In *Rhynchonella* (fig. 97 B, *c*) the brachial skeleton consists of two short curved processes. In *Terebratula* (fig. 99) there is a ribbon-like band forming a short loop. In *Stringocephalus* (fig. 101) the loop is more extensive and runs parallel to and near the margin of the valves. In *Magellania* (fig. 84 B, *l*) the loop extends nearly to the anterior margin of the shell and is then bent back upon itself. In many Palæozoic and a few Mesozoic

genera, the brachial skeleton is in the form of two spiral ribbons; in *Spirifer* (fig. 95 A) the apices of the spirals are directed towards the lateral margins of the shell, in *Glassia* they point inwards, in *Atrypa* (fig. 96 A) upwards to the centre of the dorsal surface. The brachial skeleton is absent in all the inarticulate genera, as well as in some of the articulate forms such as *Productus* and *Chonetes*.

The development of the brachial skeleton has been studied in some living species of *Terebratulina*, *Magellania*, and *Terebratella*. In *Terebratulina* the adult form is reached almost directly; but in *Magellania* the brachial skeleton passes through various stages before the adult condition is attained; and it is noteworthy that these stages are similar to the adult forms of certain other genera. Thus in *Magellania venosa* the brachial skeleton passes through stages which, in succession, resemble the brachial skeletons of the genera *Gwynia*, *Cistella*, *Bouchardia*, *Megerlina*, *Magas*, *Magasella*, and *Terebratella*, after which the adult condition is reached. Another striking fact is that some species, which have hitherto been referred to the genus *Magellania*, have a development differing from this; thus *M. cranium* passes through stages distinctive of the genera *Gwynia*, *Cistella*, *Platidia*, *Ismenia*, *Mühlfeldtia*, and *Terebratella*. If the stages through which an individual passes in its development be taken to indicate its ancestry, then it follows that in *Magellania* there are two groups of species having different ancestors, and these two groups must therefore be regarded as constituting two distinct genera (see pages 15, 16).

The largest brachiopod known is *Productus giganteus*, from the Carboniferous Limestone, which has a breadth of twelve inches; the size of the shell in different genera varies from this down to about a quarter of an inch.

Generally the shell is thin, but in some forms, such as *Daviesiella llangollensis*, it is thick and massive. The external form varies considerably; it may be globular, ovoid, hemispherical, quadrilateral, or triangular. Usually both valves are convex, but in some genera, one is plane the other convex, or one may be concave and the other convex; in the last case the space in the interior is often small. Sometimes there is a median depression or sulcus on the anterior part of one valve (generally the ventral) and a corresponding ridge on the other valve, or there may be two sulci and two ridges (biplication). The surface of the shell is sometimes quite smooth, but is often ornamented with striæ or ribs, which generally radiate from the umbones but are occasionally concentric. In a few forms the shell is covered with spines.

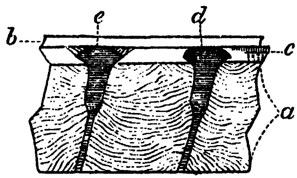


Fig. 85. Vertical section of shell of *Magellania* [= *Waldheimia*] *flavescens*, Recent. *a*, prismatic layer; *b*, chitinous layer; *c*, outer calcareous layer; *e*, *d*, canals traversing the calcareous layers. (After King.) Magnified.

In the Articulata the shell is mainly calcareous. In the genus *Magellania* it is formed of three layers (fig. 85); the inner (*a*), next the mantle, is the thickest and most important, and consists of flattened prisms of calcite arranged obliquely to the surface of the shell, each prism being encased in a membrane, which of course has disappeared in the fossil examples. The middle layer (*c*) is lamellated and also calcareous. The outer (*b*) consists

of chitinous material. The inner and middle layers are traversed by canals (figs. 85, *e*, *d*, 86) running at right angles to the surface of the shell, and containing prolongations of the mantle; in fossil specimens, in which the chitinous layer is not preserved, the openings of these canals can be seen on the surface of the shell, giving it a punctate appearance. The shell is secreted by the mantle, its outermost border producing the chitinous layer, a zone just within this forming the lamellated layer, and the remainder giving rise to the prismatic layer which gradually encroaches on the preceding; hence the last layer is the only one which can subsequently increase in thickness. In many forms the lamellated layer is absent, and in some (*e.g.* *Rhynchonella*) there are no canals traversing the calcareous layers.

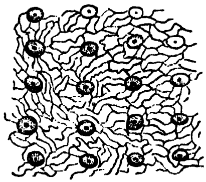


Fig. 86. Horizontal section through the prismatic layer of *Terebratula maxillata*, from the Great Oolite, showing prisms and canals. Magnified.

The shell of the Inarticulata has a different structure. In *Lingula* it consists of alternating calcareous and chitinous layers, the calcareous material being largely phosphate of lime; the canals which traverse these layers are more numerous and much smaller than those found in the articulate forms. In *Crania* the shell is calcareous and the canals branch near the surface.

The development of the shell in the Brachiopoda has been studied by Beecher. In the earliest or embryonic stage the shell is similar in character in all the genera which have been examined. This embryonic shell has been termed the *protegulum*, and may sometimes be found at the umbones of adult shells, but generally, owing to its

delicate nature, it has been worn off; it is semicircular or semi-elliptical in form, with concentric lines of growth, and is without an area; it is composed of horny material, and varies in size from ·05 to ·60 millimetre. From the constancy of the occurrence of the protegulum it has been inferred that the ancestral form of the Brachiopoda possessed throughout life a shell similar to the protegulum;

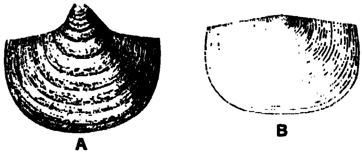


Fig. 87. *Micromitra* (*Paterina*) *labradorica*, from the Lower Cambrian (Olenellus Beds). A. Ventral valve. B. Dorsal valve. Enlarged.

but, at present, no brachiopod agreeing entirely with the protegulum has been found; for although *Paterina* (fig. 87), from the Lower Cambrian, is in many respects similar, yet the possession of an area distinguishes it from a protegulum. *Rustella*, also from the Lower Cambrian, is now regarded as the most primitive Brachiopod known.

The Brachiopoda have been divided by nearly all authors into two Classes, (1) the Inarticulata, (2) the Articulata[1], each of which may be divided into two Orders.

CLASS I. INARTICULATA

The valves are not provided with teeth, but are held together by the muscles and mantle. The intestine is long and ends in an anus. There is no brachial skeleton.

[1] These classes have received other names; the Inarticulata being known by some authors as the *Lyopomata*, the *Ecardines*, the *Pleuropygia*, or the *Tretenterata*; and the Articulata as the *Arthropomata*, the *Testicardines*, the *Apygia*, or the *Clistenterata*.

ORDER I. ATREMATA

The peduncle passes out between the umbones, the opening being shared by both valves. *E.g. Lingula.*

Lingula (fig. 88). Shell thin, nearly equivalve, compressed, elongate-ovate or quadrilateral, tapering towards the umbones, slightly gaping at the extremities. Dorsal valve a little shorter than the ventral. Hinge-line slightly thickened. Twelve muscular impressions in each valve, but usually indistinctly marked. Surface of shell smooth, or concentrically or radially striated. Peduncle long, passing out between the umbones. Shell composed of alternating layers of calcareous and chitinous material. Ordovician to present day. Ex. *L. anatina*, Recent; *L. ovalis*, Kimeridge Clay.

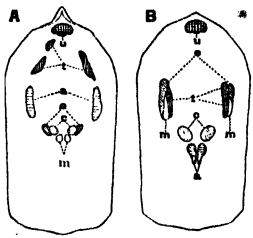


Fig. 88. *Lingula anatina*, Recent. Interior of valves showing muscular impressions. A, ventral valve. B, dorsal valve. *u*, umbonal muscle; *t*, transmedians; *c*, centrals; *a*, anterior laterals; *m*, middle laterals; *e*, external laterals. $\times \frac{1}{2}$.

Lingulella. External form similar to *Lingula*; in the ventral valve a distinct hinge-area and a groove for the peduncle. Lower Cambrian to Ordovician. Ex. *L. davisi*, Lingula Flags.

Kutorgina. Shell calcareous, usually broader than long, with a long, straight hinge-line; surface with concentric striæ. Ventral valve very convex, with an elevated umbo; four pairs of muscular impressions. Dorsal valve flat or slightly convex, with a small umbo and two pairs of muscular impressions. Area of ventral valve narrow, with a wide fissure; dorsal area only slightly developed. A rudimentary hinge. Lower (? also Middle) Cambrian. Ex. *K. cingulata.*

ORDER II. NEOTREMATA

The peduncle-opening is confined to the ventral valve. In the lower types the opening is in the form of a slit at the margin of the valve; but in the higher forms it is completely surrounded by shell, and is often near the centre of

the valve, in which case the peduncle passes out at right angles to the plane of junction of the two valves. A pseudo-deltidium is sometimes present. *E.g. Discina.*

Obolella. Shell ovate or sub-circular, lenticular, nearly equivalve. Ventral valve with a solid umbo, and a small area with a groove for the peduncle in the middle; one pair of long muscular impressions extend from near the hinge-line to the middle of the valve, between these are a pair of small impressions, and near the hinge-line a third pair of small impressions. Dorsal valve with a minute umbo, a small area, an internal median ridge, and two long muscular impressions diverging widely. Lower Cambrian. Ex. *O. crassa.*

Siphonotreta. Shell elongate-oval, biconvex, inequivalve, with spines on the surface. Hinge-line curved; no area. Ventral valve the more convex, with a prominent, straight umbo, having a small foramen at its apex continued as a tube to the interior of the valve. Dorsal valve less convex, with umbo at the margin. Muscular impressions near the hinge-line in both valves. Ordovician and Silurian. Ex. *S. micula*, Llandeilo.

Discina (group). Shell composed partly of chitinous material; sub-orbicular, or sub-elliptical, surface smooth or covered with striæ of growth. Valves more or less conical, the summits of both sub-central or sub-posterior. Peduncle-opening placed either near the summit of the ventral valve or a little behind it. Four adductor impressions. Cambrian to present day. *Discina*, in the wide sense, as defined above, includes the three genera *Discina* (restricted), *Discinisca*, and *Orbiculoidea.*

Discina (restricted). Both valves convex. Peduncle-opening small, near the middle of the valve externally, passing through the shell obliquely forwards. The only species definitely known is *D. striata*, Recent.

Discinisca. Ventral valve flattened; behind the apex is a disc, which is depressed externally and interrupts the continuity of the lines of growth. The disc is perforated for the peduncle by a fissure which passes directly, not obliquely, through it. Tertiary and living; perhaps Mesozoic. Ex. *D. lamellosa*, Recent.

Orbiculoidea. Ventral valve flattened: on the surface just

behind the apex is a narrow furrow, which is perforated at the point farthest from the apex, the perforation passing through the shell obliquely backwards. Cambrian to Carboniferous, perhaps also Mesozoic. Ex. *O. morrisi*, Wenlock Limestone.

Crania (fig. 89). Shell calcareous, traversed by vertical canals which branch near the outer surface: quadrangular or sub-circular, smooth or with radiating ribs, fixed by the ventral valve: without peduncle-opening. Ventral valve depressed-conical: dorsal larger than the ventral, conical with a sub-central apex. Interior of each valve with a border covered with granulations. Two pairs of well-marked adductor impressions in each valve (a, a'): the posterior pair

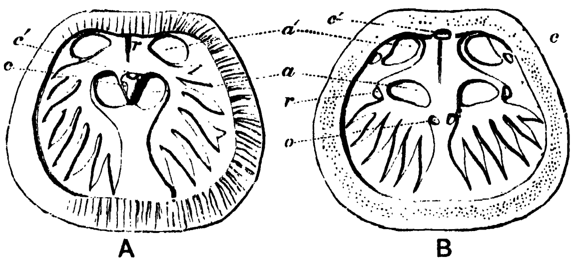


Fig. 89. *Crania anomala*, Recent. A. Interior of ventral valve. B. Dorsal valve. a, anterior adductors; a', posterior adductors; c, posterior adjustors; c', cardinal muscle; r, o, central and external adjustors. (From Woodward.) ×2.

near the margin, the anterior near the centres of the valves and close together, especially so in the ventral valve; also other smaller muscular impressions. A triangular protuberance near the centre of the ventral valve. Ordovician to present day. Ex. *C. ignabergensis*, Chalk.

CLASS II. ARTICULATA

The valves articulate by means of two teeth on the ventral valve which fit into sockets on the dorsal. The intestine is short and ends blindly. A brachial skeleton may or may not be present.

ORDER I. PROTREMATA

A pseudo-deltidium is developed, but sometimes disappears in the adult. The peduncle-opening is at the margin of the ventral valve, in the form of a fissure (delthyrium) either entirely open or more or less completely closed by the pseudo-deltidium. Usually there is no brachial skeleton. This group is found mainly in the Palæozoic formations; the only living form is *Thecidea* (*Lacazella*). *E.g. Orthis.*

Productus (fig. 90). Shell free, or fixed by spines, generally transverse (*i.e.* broader than long) but sometimes elongated, often produced into 'ears' at the sides. Dorsal valve concave. Ventral valve very convex, often sharply bent, sometimes with a median sinus; umbo large, incurved, not perforated. Hinge-line straight, teeth absent or rudimentary. Area linear or absent. Surface orna-

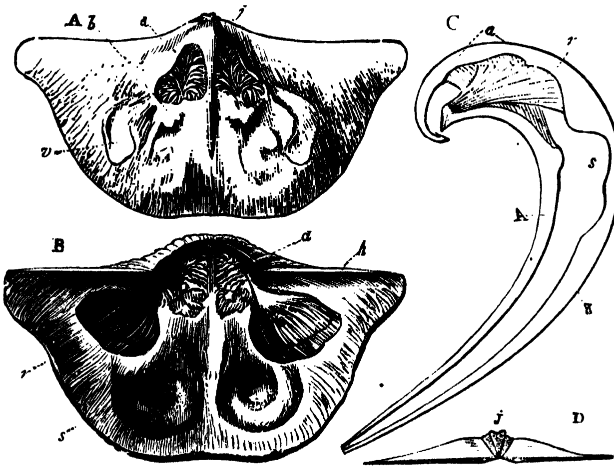


Fig. 90. *Productus giganteus*, Carboniferous Limestone. A. Interior of dorsal valve. B. Interior of ventral valve. C. Ideal section of both valves. D. Dorsal hinge-line. *j*, cardinal process; *a*, adductor; *r*, divaricator; *h*, ventral area; *b*, brachial prominence (?); *s*, hollows occupied by the spiral arms; *v*, reniform impressions. (From Woodward.) × ⅓.

mented with radiating ribs, crossed by concentric folds, especially in the umbonal region. Tubular spines, especially in the region of the umbo and ears. Muscular impressions strongly marked; in the ventral valve the adductors (*a*) are near the umbo, and in front of them are the divaricators (*r*). A prominent cardinal process (*j*) on the dorsal valve is continued as a median ridge in the interior. No brachial skeleton. Carboniferous and Permian. Ex. *P. semireticulatus*, Carboniferous Limestone. *Productella*, Devonian, is an allied form.

Strophalosia. Shell similar to *Productus* in form; attached by umbo of ventral valve. A distinct area on each valve, with a pseudo-deltidium; the ventral area larger than the dorsal. Ventral valve with two prominent teeth. Dorsal valve with a prominent, bifid cardinal process. Surface of ventral (and sometimes also the dorsal) valve covered with spines. Middle Devonian to Permian. Ex. *S. excavata*, Permian.

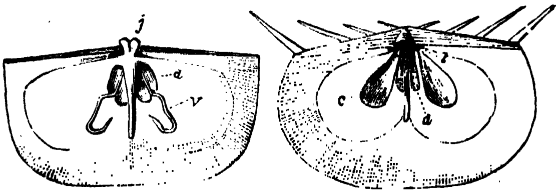


Fig. 91. *Chonetes*, from the Devonian. A, dorsal; B, ventral valve. *a*, adductor impressions; *c*, divaricators; *t*, teeth; *v*, vascular impressions; *j*, cardinal process. (From Woodward.) Enlarged.

Chonetes (fig. 91). Shell transverse, semicircular, concavo-convex, or sometimes plano-convex. Hinge-line straight, forming the greatest width of the shell. Teeth strong An area on each valve; dorsal area very narrow. Upper margin of area of ventral valve with a row of hollow, diverging spines, which increase in length towards the ends of the hinge-line. Delthyrium more or less completely closed by a pseudo-deltidium. Muscular impressions faintly marked. Cardinal process divided. Surface usually ornamented with radial striæ. Silurian to Permian. Ex. *C. striatella*, Upper Ludlow.

Leptæna. Shell concavo-convex, semi-oval or nearly quadrangular, ornamented with small radiating ribs, crossed by concentric

folds on the flatter parts; anterior part bent sharply, often at a right angle to the posterior part. Space between the two valves very small. Hinge-line straight, forming the greatest width of the shell. A narrow area on each valve; the delthyrium of the ventral valve covered by a convex pseudo-deltidium. Umbo of ventral valve perforated by a small foramen except in old individuals. Two strong diverging teeth in the ventral valve supported by lamellæ which are continued round the muscular area. Muscular impressions: in the ventral valve, two narrow adductors surrounded by two large divaricators; in the dorsal, two small adductors near the centre of the valve, behind which are two larger adductors. Cardinal process divided. Ordovician to Carboniferous. Ex. *L. rhomboidalis*, Bala Beds, etc.

Strophonella. Shell semicircular or semi-elliptical; ventral valve concave, dorsal valve convex. Hinge-line long, straight. Dorsal area narrower than the ventral; inner margins of areas crenulate. Muscular area of ventral valve limited by a prominent border. Silurian and Devonian. Ex. *S. euglypha*, Wenlock Limestone.

Strophomena. Shell semicircular or semi-elliptical, ornamented with fine radiating ribs; hinge-line straight, forming the greatest width; dorsal valve convex; ventral valve convex near the umbo, but concave in the middle. Ventral area conspicuous, with a pseudo-deltidium; apex perforated except in old age; dorsal area narrow. Teeth diverging widely, supported by plates, which are produced into ridges nearly surrounding the muscular area; the latter is divided by a median ridge. Dorsal valve with a ridge separating two large adductor impressions, in front of which are two narrow impressions. Ordovician and Silurian. Ex. *S. antiquata*, Wenlock Limestone.

Schellwienella. Ventral valve flat or slightly concave, with a slight convexity around the umbo; dorsal valve convex. Valves ornamented with fine radiating ribs; hinge-line usually shorter than the width of the shell. Without a median septum. Ventral area prominent, often high, the two sides sometimes unequal; delthyrium closed by a pseudo-deltidium; muscular impressions fan-shaped; dental plates short, diverging. Dorsal area rudimentary or absent; the cardinal process fairly strong. Carboniferous. Ex. *S. crenistria*, Carboniferous Limestone.

Orthis (group). (Figs. 92, 93.) Outline sub-circular or quadrate. Both valves more or less convex. Surface radially ribbed or striated. Hinge-line straight, sometimes equal to the width of the shell, but generally shorter. An area on each valve, each usually divided by an open delthyrium. In the ventral valve two large teeth, supported by dental plates. Four muscular impressions in the dorsal valve. Two long, narrow impressions (*d*) with two smaller ones (*a*) between them in the ventral. Cambrian to Carboniferous. *Orthis*, as defined above, includes a large number of species which have been divided

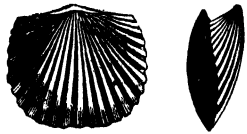
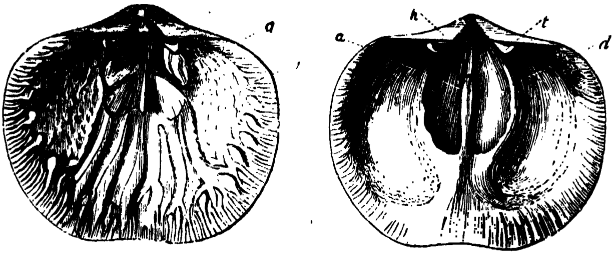


Fig. 92. *Orthis calligramma* var. *Davidsoni*, Ordovician. (From Nicholson.)



A B

Fig. 93. *Orthis* (*Schizophoria*) *striatula*, Devonian. A. Interior of dorsal valve. B. Ventral valve. *c*, curved brachial processes (crura); *v*, genital impressions; *h*, area with delthyrium; *t*, teeth; *a*, adductors; *d*, divaricators. (From Woodward.) Natural size.

into several groups now regarded as sub-genera or genera, some of which are *Orthis* (restricted), *Platystrophia*, *Dalmanella*, *Schizophoria*, *Rhipidomella*, *Bilobites*; four of these are briefly described below:

Orthis (restricted) (fig. 92). Shell plano-convex; with few strong sharp ribs, rarely bifurcating. Area of the ventral valve elevated. Cardinal process in the form of a thin vertical plate extending from the apex to the base of the delthyrium. A small flat plate sometimes found in the apex of the delthyrium. Shell not punctate. Ordovician to Silurian. Ex. *O. callactis*, *O. calligramma*, Ordovician.

Platystrophia. Shell spiriferoid in form, with long hinge-line, and sharp radial folds; both valves very convex, with the two areas of nearly equal size. Ventral valve with a strong median fold, dorsal

valve with a corresponding sinus. Cardinal process a simple linear ridge. Shell not punctate; surface finely granular. Ordovician and Silurian. Ex. *P. lynx*, Ordovician.

Dalmanella. Shell punctate, ornamented with fine, bifurcating striæ. Hinge-line generally shorter than the width of the shell. Ventral valve usually more convex than the dorsal, with an elevated umbo. Teeth prominent, supported by lamellæ. Ordovician to Devonian. Ex. *D. elegantula*, Silurian.

Schizophoria (fig. 93). Shell punctate, ornamented with fine hollow striæ bearing short spines. Dorsal valve more convex than the ventral. Hinge-line shorter than the width of the shell. Cardinal process with accessory ridges in old individuals. Dorsal valve with 4 to 6 deep pallial sinuses (fig. 93 A). Silurian to Upper Carboniferous. Ex. *S. resupinata*, Carboniferous.

Pentamerus (fig. 94). Shell oval, or subtrigonal, biconvex, ornamented with ribs, rarely smooth. Ventral valve the more

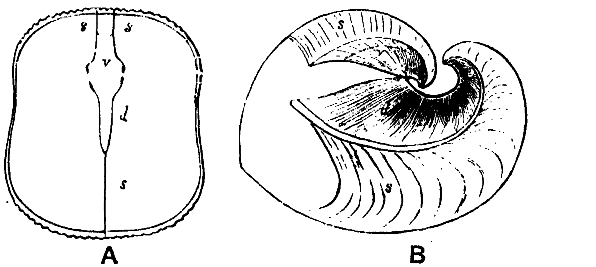


Fig. 94. *Pentamerus* (*Conchidium*) *knighti*, Aymestry Limestone. A. Transverse section. B. Longitudinal section. *s*, septa; *d*, dental plates. (From Woodward.) $\times \frac{1}{2}$.

convex. Median dorsal fold and ventral sinus slightly developed or absent. Umbo of ventral valve large, sharp, often strongly incurved, usually touching the dorsal valve and concealing the delthyrium. No area and usually no pseudo-deltidium; hinge-line curved. Dental plates (*d*) trough-like, converging in the ventral valve to form a large median septum (*s*); in the dorsal valve two septa close together (*s*–*s*). Silurian to Devonian. *Pentamerus* (restricted) includes species with a smooth shell or with only faint radiating folds. Ex. *P. oblongus*,

Llandovery. *Conchidium* includes species with numerous strong radial ribs. Ex. *C. knighti*, Aymestry Limestone. *Gypidula* is similar to *Pentamerus*, but with a median dorsal fold and ventral sinus; surface with folds or nearly smooth. Ex. *G. galeata*, Wenlock Limestone. *Sieberella* is distinguished from *Gypidula* by the presence of an area on the ventral valve. Ex. *S. comis*, Devonian.

Stricklandia. Shell large, oval, ornamented with ribs; valves nearly equal, sometimes with a fold and a sinus. Umbo of ventral valve not prominent. Hinge-line straight; an area on each valve, the dorsal being small. A short median septum in the ventral valve from which arise two plates forming a small chamber under the umbo. Silurian. Ex. *S. lens*, Llandovery Beds.

Camarophoria. External form similar to *Rhynchonella*, with radial folds; ventral umbo sharp, incurved. In the ventral valve the dental plates converge to form a short trough supported by a long medium septum. In the dorsal valve there is a trough-like plate supported by a septum. Carboniferous and Permian. Ex. *C. schlotheimi*, Permian.

ORDER II. TELOTREMATA

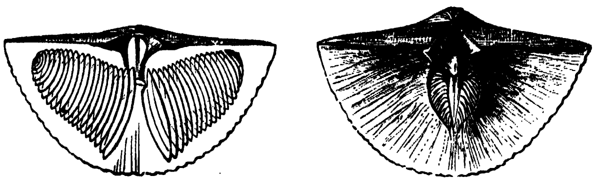
The peduncle-opening is confined to the ventral valve in the adult, and is either at the umbo or beneath it. A deltidium is developed, and a brachial skeleton is present. *E.g. Magellania.*

Spirifer (fig. 95). Shell transverse, more or less triangular, usually alate, biconvex, ornamented with ribs radial. Often with a sinus on the ventral valve and a ridge on the dorsal. Hinge-line straight, long. An area on each valve, the ventral one triangular, often transversely striated, with a delthyrium which is partly closed by a deltidium; dorsal area small. Teeth supported by short dental plates. Brachial skeleton often filling a great part of the interior of the shell, formed mainly of two spirals, with their apices directed laterally. Silurian to Permian. Ex. *S. striatus*, Carboniferous Limestone. *Martinia* includes 'Spirifers' with a short hinge, usually smooth surface, and without dental plates (*e.g. M. glaber*, Carboniferous).

Spiriferina. Similar to *Spirifer*, with a high median septum in the ventral valve, and a punctate shell. Carboniferous to Lias. Ex. *S. walcotti*, Lias.

Syringothyris. Similar to *Spirifer*, but with a high ventral area and an internal tube in the delthyrium. Carboniferous. Ex. *S. cuspidata.*

Cyrtia (fig. 83). Area on the ventral valve very large; deltidium narrow, convex, with a perforation. Dental plates well developed but not joining. Brachial skeleton as in *Spirifer*, but the apices of the spires are nearer the hinge-line. Silurian and Devonian. Ex. *C. exporrecta*, Wenlock Limestone.



A B

Fig. 95. *Spirifer striatus*, Carboniferous. A. Interior of dorsal valve, showing brachial skeleton. B. Interior of ventral valve, showing muscular impressions, area, and delthyrium. (From Woodward.) × ½.

Uncites. Shell elongate-oval, biconvex, striated. Hinge-line curved, no area. Umbo of ventral valve prominent and incurved, often distorted; peduncle-opening closed in the adult by a concave deltidium. Dental plates strong. Apex of dorsal valve incurved and partly hidden in the ventral valve; cardinal process prominent. Brachial skeleton spiral, apices of spires directed laterally. Devonian. Ex. *U. gryphus.*

Meristina. Shell biconvex, smooth; hinge-line curved, no area. Ventral umbo incurved in the adult, so as to conceal the foramen. Teeth supported by dental plates which reach to near the middle of the valve. Spires of brachial skeleton pointing laterally, joined by a band bearing a median stem which is forked at its end. Silurian. Ex. *M. tumida.*

Athyris. Shell with transversely elliptical or sub-circular outline and a median sinus; the two valves nearly equally convex. Surface often with concentric growth-lines produced into lamellæ.

Hinge-line curved. Ventral umbo small, incurved, usually concealing the peduncle-opening and deltidium; with prominent teeth supported by dental plates; four muscular impressions. Dorsal valve with a tube from the interior of the valve opening at the hinge. Brachial skeleton consisting of two spires joined by a band; the apices of the spires pointing laterally. Devonian and Carboniferous. Ex. *A. concentrica*, Devonian.

Atrypa (fig. 96). Shell sub-circular or oval, ornamented with radiating ribs, often crossed by well-marked growth-rings. Ventral valve convex near the umbo, depressed in front; dorsal valve often much inflated. Hinge-line short, slightly curved; no area. Ventral valve with a small circular foramen, a small deltidium, and two strong crenulate teeth; muscular impressions grouped at the centre of the valve. Brachial skeleton formed of two spirals with their apices directed towards the centre of the dorsal valve; the two spires joined by a band near the umbo. Ordovician to Devonian; abundant in Silurian and Devonian. Ex. *A. reticularis*, Wenlock Limestone.

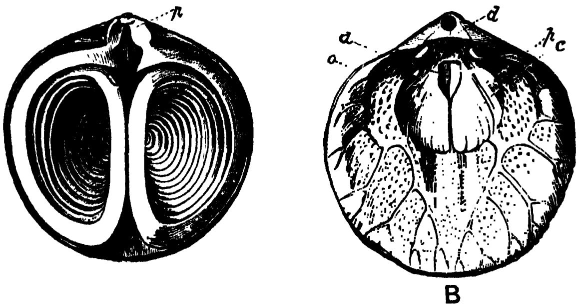


Fig. 96. *Atrypa reticularis*, Wenlock Limestone. A. Dorsal valve, showing brachial skeleton. B. Interior of ventral valve. *a*, impressions of adductor muscles; *c*, divaricator muscles; *p*, muscles of peduncle; *o*, genital impression; *d*, deltidium. (From Woodward.) Natural size.

Rhynchonella. Shell round, oval or triangular, not perforated by canals, usually ornamented with numerous radial ribs. Both valves convex; usually a median sinus on the ventral valve and a corresponding ridge on the dorsal. Ventral umbo small, acute, more or less incurved; foramen below the umbo, almost surrounded by

the deltidium. Ventral valve with two strong teeth, supported by dental plates; muscular area oval—two large divaricator impressions enclosing small adductors. Brachial skeleton reduced to two short, free lamellæ; no cardinal process; a median septum in the dorsal valve. Trias to Chalk. *Rhynchonella* in a very restricted sense includes forms with the radial ribs little developed; with a sub-pyramidal shell; the sinus on the ventral valve becoming broad and deep in front where it often produces a prominent tongue-shaped extension; the dorsal valve with a corresponding ridge or fold. Upper Jurassic. Ex. *R. loxia*. *Cyclothyris* includes the majority of the Mesozoic species usually referred to *Rhynchonella*, and differs from *Rhynchonella* (restricted) mainly by the numerous, well developed radial ribs, and by the smaller development of the median sinus and ridge. Abundant in Jurassic and Cretaceous. Ex. *C. latissima*, Lower Greensand.

Acanthothyris. Differs from *Cyclothyris* mainly by the development of numerous spines all over the surface of the shell. Ventral sinus and dorsal fold usually little developed. Jurassic to present day; mainly Jurassic. Now living in the seas around Japan. Ex. *A. spinosa*, Inferior Oolite.

Hemithyris (fig. 97). Form similar to *Acanthothyris*. Shell smooth or faintly ribbed. Ventral umbo high, with the deltidium poorly developed. No dental plates. Pliocene to present day. Ex. *H. psittacea*.

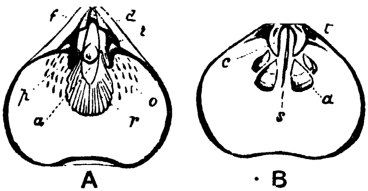


Fig. 97. *Hemithyris psittacea*, Recent. A, interior of ventral; B, interior of dorsal valve. *f*, foramen; *d*, deltidium; *t*, teeth; *a*, adductor impressions; *r*, divaricator impressions; *p*, peduncular impressions; *o*, genital impressions; *t'*, dental sockets; *c*, brachial skeleton; *s*, septum. (From Woodward.) Natural size.

Most of the Palæozoic species formerly referred to *Rhynchonella* are now regarded as belonging to distinct genera, viz.:—*Rhynchotreta*, *Camarotœchia*, *Wilsonia*, *Uncinulus*, *Hypothyridina* (= *Hypothyris*), *Pugnax*.

Pugnax (fig. 98). Ventral valve shallow, dorsal valve deep. Median sinus and fold very prominent, causing the front margin to be elevated and often acuminate. Some radial ribs present. Dental plates short. No median septum in the dorsal valve. Devonian and Carboniferous. Ex. *P. acuminatus*, Carboniferous Limestone.

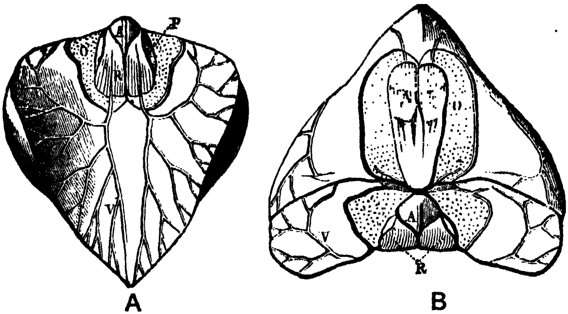


Fig. 98. *Pugnax acuminatus*, Carboniferous Limestone. Internal casts. A. Ventral valve. B. Dorsal valve and posterior part of ventral. *V*, 'vascular' impressions; *O*, genital impressions; *A*, adductors; *R*, divaricators; *P*, muscles of the peduncle. (From Woodward.) Natural size.

Terebratula (figs. 82, 86, 99). Shell biconvex; oval, elongate or rounded; surface nearly always smooth; often with two folds on the dorsal valve and two corresponding sinuses on the ventral. Hinge-line curved. Umbo of ventral valve truncated by a circular foramen with a deltidium at its base. Brachial skeleton in the form of a short loop extending only about a third the length of the shell. Jurassic to present day. Ex. *T. phillipsi*, Inferior Oolite; *T. bisinuata*, Eocene.

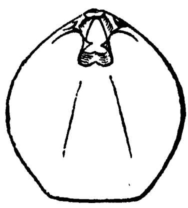


Fig. 99. *Terebratula* (*Liothyrina*) *vitrea*, Recent. Interior of dorsal valve, showing the brachial skeleton. (From Woodward.) × ⅔.

Terebratula is also used in a more restricted sense which excludes the Mesozoic species from that genus.

Dictyothyris (Jurassic) is similar to *Terebratula*, but with fine radial ribs and concentric lines; ex. *D. coarctata*. *Dielasma* (Devonian

to Permian) and *Cœnothyris* (Trias) are distinguished from the *Terebratulæ* of Jurassic and later formations mainly by the possession of well-developed dental plates. Ex. *Dielasma hastatum*, Carboniferous; *Cœnothyris vulgaris*, Trias.

Terebratulina (fig. 100). Form similar to *Terebratula*. Ornamented with fine radiating ribs. Umbo short, foramen large, deltidium small. Two ear-like processes at the sides of the dorsal umbo. Brachial loop short, with a ring formed by a band between the two branches. Jurassic to present day. Ex. *T. striata*, Chalk.

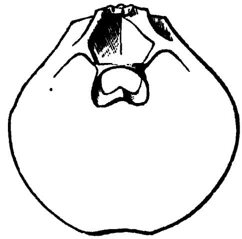


Fig. 100. *Terebratulina caput-serpentis*. Interior of dorsal valve. Recent. (From Woodward.) ×2.

Magellania (= *Waldheimia*) (fig. 84). Distinguished from *Terebratula* by the longer brachial loop, extending to at least half the length of the shell, and by a median septum in the dorsal valve, which is, however, sometimes rudimentary. The shell may be smooth, or with folds, or radially ribbed. Lias to present day. Ex. *M. flavescens*, Recent.

Magellania in the restricted sense includes species of the type of the recent *M. flavescens* in which there are radial folds on the shell. A large number of species are found in the Mesozoic rocks and differ in some respects from the typical forms of *Magellania*; they have been divided into several groups; by some authors these divisions are regarded as genera or sub-genera, some of the more important being:—*Eudesia* (ex. *E. cardium*, Great Oolite); *Zeilleria* (ex. *Z. cornuta*, Lias); *Ornithella* (= *Microthyris*) (ex. *O. ornithocephala*, Cornbrash); *Aulacothyris* (ex. *A. resupinata*, Lias).

Terebratella. Shell oval, usually with radiating ribs. Ventral valve very convex; dorsal more or less flattened. Hinge-line straight or slightly curved; an area present. Umbo with a large foramen, and deltidium below. Brachial skeleton similar to *Magellania*, but descending branches joined by a band to a septum in the middle of the dorsal valve. Lias to present day. Ex. *T. pectita*, Upper Greensand.

Stringocephalus (fig. 101). Shell smooth, circular or oval in outline. Ventral valve with a sharp, prominent, incurved umbo; area present. Peduncle opening large in young individuals, but smaller and oval in adults on account of the development of the deltidium. Ventral valve with a median septum (*vs*), which extends from the umbo almost to the front of the valve, and increases in

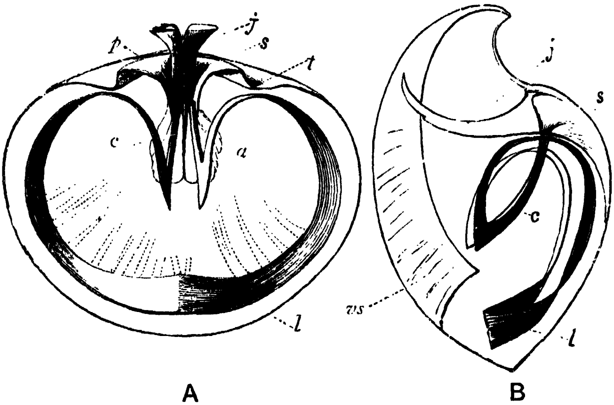


Fig. 101. *Stringocephalus burtini*, Devonian. A. Dorsal valve. B. Profile. *a*, adductor; *c*, crura; *l*, loop; *j*, cardinal process; *p*, hinge-plate; *s*, dorsal septum; *vs*, ventral septum; *t*, dental sockets. (From Woodward.) $\times \frac{1}{2}$.

height towards the latter. Dorsal valve less convex, with a small septum (*s*), and a long slightly curved cardinal process (*j*), divided at its extremity to embrace the ventral septum. The brachial skeleton consists of two branches (*c*) arising from the hinge-plate (*p*), which pass to the middle of the shell and are then sharply bent back and form a ring (*l*) parallel and near to the margin of the valve. Devonian. Ex. *S. burtini.*

Distribution of the Brachiopoda

The Brachiopods are all marine, and are found in all parts of the world. At the present time they are much less numerous than in former periods of the earth's history,

there being only about 158 living species belonging to 33 genera; of these species 29 are Inarticulates, 129 Articulates. Of the latter group two species belong to the Protremata and 127 to the Telotremata—this being the predominating group of Brachiopods at the present day and represented by 15 Rhynchonellids and 112 Terebratulids. Many forms occur more abundantly where the sea-bottom is rocky, or stony, or formed of corals, than where it is soft and muddy; frequently they are much localised, being found in enormous numbers at one spot, whilst, in the adjoining areas, they are sparsely distributed. Over 70 per cent. of the existing species are found between the shore-line and a depth of 100 fathoms, and several of these do not extend beyond this limit. Brachiopods are most abundant between 15 and 100 fathoms; their relative scarcity in the Littoral zone (p. 266) is probably due to the fact that most of them are attached by the peduncle and would easily become displaced in the rough waters of the shallow sea. As a whole the Brachiopoda are characteristic of shallow water. Below 150 fathoms they soon become comparatively rare; but some species occur in deep water and in abyssal regions down to 2900 fathoms and are characterised by their thin shells.

The majority of the Inarticulata are found between low-water mark and a depth of 15 fathoms; of the remainder, all but one occur between 15 and 100 fathoms. The principal littoral genera are *Lingula* and *Discina*, which extend from the shore-line to a depth of about 10 fathoms. The littoral and shallow water species characterise warm seas, and are more numerous and possess thicker and often larger shells than those found in deep water and abyssal regions. *Crania* ranges from 2 to 800 fathoms and is the only Inarticulate genus living in the

shallow water of cooler regions, mainly those of the Northern Hemisphere.

The Articulata, although represented by 15 species in water of less than 15 fathoms deep, are mainly characteristic of depths between 15 and 100 fathoms. The Rhynchonellids do not live at depths of less than 15 fathoms and are found mainly in deep water; they occur in nearly all parts of the oceans from the Arctic to the Antarctic regions; some of the species are found in warm seas but the majority live in cool waters; some species have a restricted geographical range, others occur in several provinces, and one (*Hemithyris psittacea*) is found throughout the greater part of the Northern Hemisphere. In depth *Hemithyris* ranges from 15 to 2084 fathoms. The Terebratulids are most abundant, both in individuals and species, between the shore-line and a depth of 100 fathoms, where 67 per cent. of the species are found.

Geographically, the Brachiopoda which live in comparatively shallow water are distributed in provinces, agreeing generally with the Molluscan provinces (p. 268), and these can be grouped into larger regions. Each province is characterised by the presence or abundance of certain species, the ranges of which are determined mainly by climate. A few species, as for example *Terebratulina caput-serpentis*, have a very wide geographical distribution, extending from polar to tropical regions, and also have a great range in depth, the form mentioned being found from the shore-line down to 1180 fathoms.

The species found in deep water have generally a much wider geographical range than those confined to shallow water; and the polar or boreal species have a wider range than those found in warmer regions, since, in lower latitudes, they can find a suitable temperature at greater depths.

Brachiopods are very abundant in the Palæozoic and Mesozoic formations, and are usually well-preserved on account of the fact that their shell generally consists of calcite. Of the 33 living genera not less than 23 are represented among fossil forms; of these *Lingula* and *Crania* have existed since the Ordovician period, and several others (*e.g. Acanthothyris, Megathyris, Terebratella, Terebratulina*) since Jurassic times. In connection with the remarkably long range in time of *Lingula* it is interesting to note the habitat of the living species. *Lingula* lives in tubes which it burrows in the sediment on the sea-floor, and is attached to the tube by means of the peduncle; it survives when left uncovered by the sea for several hours, and can live in places which have become putrid owing to the decomposition of organic matter; further, when buried bya rapid deposit of sediment which kills molluscs and other brachiopods, *Lingula* survives by tunnelling to the surface.

The earliest Brachiopods occur in the Lower Cambrian (*Olenellus* Beds), where at least nineteen genera are represented, of which *Lingulella, Paterina, Kutorgina,* and *Obolella* may be mentioned. The majority of the species found in the Cambrian belong to the Inarticulata; the Protremata are also represented, but do not become important until the Upper Cambrian. In the Ordovician System the Brachiopods (especially the Articulata) are much more numerous than in the Cambrian, and the Telotremata make their first appearance in the Middle Ordovician. The Brachiopods attain their maximum development in the Ordovician and Silurian ; their decline begins in the Devonian; in the Mesozoic it is especially marked by the reduction in the number of genera, but the Telotremata are abundantly represented. The chief genera met with in the different systems are:—

Cambrian. *Rustella*, *Micromitra*, *Obolus*, *Lingulella*, *Lingulepis*, *Kutorgina*, *Obolella*, *Orbiculoidea*, *Acrotreta*, *Eoorthis*.

Ordovician. *Lingula*, *Lingulella*, *Siphonotreta*, *Orthis*, *Platystrophia*, *Strophomena*, *Leptæna*.

Silurian. *Lingula*, *Orbiculoidea*, *Atrypa*, *Orthis*, *Dalmanella*, *Meristina*, *Spirifer*, *Cyrtia*, *Rhynchotreta*, *Camarotœchia*, *Wilsonia*, *Pentamerus*, *Conchidium*, *Gypidula*, *Stricklandia*, *Leptæna*, *Strophonella*, *Strophomena*, *Chonetes*.

Devonian. *Uncites*, *Stringocephalus*, *Athyris*, *Atrypa*, *Dalmanella*, *Schizophoria*, *Rhipidomella*, *Spirifer*, *Sieberella*, *Uncinulus*, *Hypothyridina*. The first two are confined to the Devonian.

Carboniferous. *Lingula*, *Orbiculoidea*, *Crania*, *Schellwienella*, *Chonetes*, *Athyris*, *Orthis* (*Schizophoria*), *Spirifer*, *Martinia*, *Syringothyris*, *Productus*, *Dielasma*, *Pugnax*. *Spirifer* and *Productus* are particularly abundant.

Permian. *Productus*, *Strophalosia*, *Camarophoria*, *Spirifer*, *Dielasma*.

Mesozoic. Most of the important Palæozoic genera die out before the commencement of the Mesozoic period, but two forms allied to Palæozoic types are found in the Lias, viz. :—*Spiriferina* and *Cadomella*. The Mesozoic period is remarkable for the extraordinary abundance of *Terebratula*, *Magellania*, *Rhynchonella*, and their allies. Other genera which occur are *Lingula*, '*Discina*,' *Crania*, *Thecidea*, *Terebratulina*, and *Terebratella*—the last four are more abundant in the Cretaceous than in the Jurassic; in the former *Magas* and *Kingena* also occur. *Koninckina* is confined to the Trias.

Tertiary. Brachiopods are very poorly represented ; the following genera, all of which have living representatives, occur in Tertiary deposits, but are not common :—*Lingula*, *Terebratula*, *Terebratulina*, and *Magellania*.

PHYLUM POLYZOA

Classes.	*Orders.*	*Sub-Orders.*
1. Ectoprocta	1. Phylactolæma.	
	2. Gymnolæma ...	1. Cyclostomata.
		2. Trepostomata.
		3. Cryptostomata.
		4. Cheilostomata.
		5. Ctenostomata.
2. Entoprocta.		

WITH the exception of the genus *Loxosoma* all the Polyzoa[1] are colonial animals, numerous individuals living in association. The colony is nearly always fixed, and may be arborescent, laminar, almost massive, or encrusting shells, stones, or plants. The entire colony is known as the *zoarium*; each individual (fig. 102 A) has a sac-like form; at the upper end there is a platform or disc, the *lophophore*, on which tentacles (*t*) are placed, arranged either in a circle or in the form of a horse-shoe. In most forms the tentacles are not contractile, but are provided with cilia, which produce a current of water that conveys food to the mouth (*o*). The anal aperture (*a*) is near the mouth, generally below the lophophore, but in some forms within the circle of tentacles. On account of this approximation of the mouth and anus the alimentary canal is bent into a U-shape; in it may be distinguished œsophagus (*oes*), stomach (*st*), and intestine (*int*). Between the alimentary canal and the body-wall is a spacious body-cavity. The nervous system

[1] The name *Bryozoa* is used for this Phylum by many authors.

consists of a single ganglion (*g*) placed on the side of the œsophagus facing the intestine. The polyzoa multiply by budding and sexually, and are generally hermaphrodite. Heart and blood-vessels are absent.

The structures described above form together what is known as the *polypide*; this is contained in the body-wall

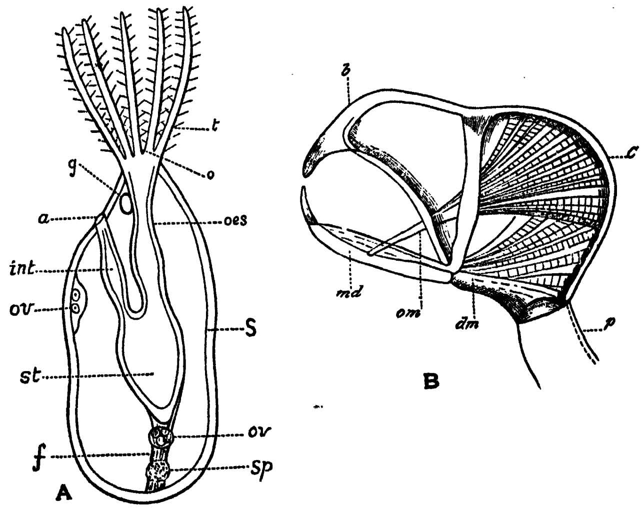


Fig. 102. A. Diagram of the structure of a single Polyzoan individual. *S*, body-wall; *t*, tentacles; *o*, mouth; *oes*, œsophagus; *st*, stomach; *int*, intestine; *a*, anus; *g*, ganglion; *f*, funiculus; *ov*, ovary; *sp*, testis. B. Avicularium of *Bugula*, enlarged. *b*, beak; *md*, mandible; *C*, chamber; *p*, peduncle; *om*, occlusor muscles; *dm*, divaricator muscles. (After Hincks.)

or *zoœcium*. The outer layer of the zoœcium, known as the *ectocyst*, generally becomes hardened by calcareous or chitinous matter, and after the death of the animal this alone remains; its surface is usually ornamented with ribs etc. The anterior part of the polypide can be withdrawn by means of longitudinal muscles into the zoœcium, just

as the finger of a glove can be pulled into the hand. In some Polyzoa (the Cyclostomata, etc., fig. 103 B) the zoœcium, is tube-like, the aperture is at the end and is of the same diameter, or nearly so, as the rest of the tube. In others (the Cheilostomata, fig. 103 A) the zoœcium is more or less box-shaped, the aperture (*m*) is contracted and is not terminal, but is situated in front near the anterior end, and is provided with a movable lid or operculum. In many of the Cheilostomata there is at the anterior end of the zoœcium, above the aperture, a pro-

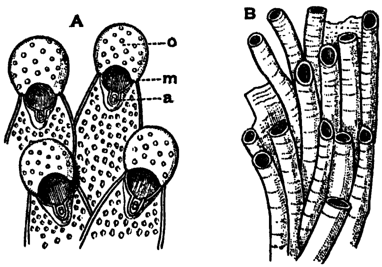


Fig. 103. A. Portion of *Smittia landsborovi*, a Cheilostomatous Polyzoan, Recent. *o*, oœcium; *m*, aperture of the zoœcium; *a*, avicularium. B. Portion of *Tubulipora fimbria*, a Cyclostomatous Polyzoan, Recent. Enlarged.

jecting chamber (*o*), termed the *ovicell*, into which the ova pass. In many forms of Cheilostomata some of the individuals are modified so as to form appendages termed *avicularia* and *vibracula*. The avicularium (fig. 102 B) may be sessile or placed on a peduncle (*p*), and in the more specialized forms has somewhat the appearance of a bird's head, consisting of a chamber (*C*) produced into a beak anp provided with a mandible (*md*) which is kept constantly snapping by means of muscles in the chamber. The vibraculum consists of a long seta kept in motion by means of muscles at its base. The individuals of a colony may com

municate with one another, either directly, or by means of *communication-plates*; these are portions of the zoœcium which are thinner and perforated. The surface of the zoœcium may be smooth or punctate, or ornamented with spines, granules, or ribs.

The Polyzoa are divided into two classes, (1) the Ectoprocta, (2) the Entoprocta. The Ectoprocta only are found fossil.

CLASS I. ECTOPROCTA

The anal aperture is not situated within the area of the lophophore. There are two orders, (1) the Phylactolæma, (2) the Gymnolæma.

ORDER I. PHYLACTOLÆMA

The lophophore is horse-shoe-shaped. There is a tongue-shaped lip in front of the mouth, known as the epistome. The forms included in this order are found only in fresh-water and do not occur fossil.

ORDER II. GYMNOLÆMA

The lophophore is circular, and there is no epistome. There are five sub-orders, (1) Cyclostomata, (2) Trepostomata, (3) Cryptostomata, (4) Cheilostomata, (5) Ctenostomata. The last is not known in the fossil state; the second and third are extinct.

SUB-ORDER 1. CYCLOSTOMATA

The zoœcia are calcareous and tubular, and seldom divided by transverse partitions; as a rule all are of one size, since mesopores, acanthopores, avicularia, and vibracula are generally absent; the apertures are round and terminal, not constricted and not provided with an operculum. There may be a brood-pouch, formed of one or

more modified zoœcia. Such a brood-pouch is called an *oœcium*, and is a *gonœcium* if composed of one, or a *gonocyst* if of more than one zoœcium. But ovicells, such as are characteristic of the Cheilostomata, and are not modified individuals, are never present.

Stomatopora. Zoarium encrusting, of branching rows of zoœcia in single file. Ordovician to present day; common in Jurassic and Cretaceous. Ex. *S. granulata*, Cretaceous.

Berenicea. Zoarium a thin, flat, encrusting sheet—discoid, fan-shaped, or irregular. Zoœcia simple, tubular, arranged in irregularly alternating lines. Ordovician to present day—common in the Jurassic and Cretaceous. Ex. *B. diluviana*, Lias to Oxfordian.

Idmonea. Zoarium encrusting or erect. Zoœcia arranged in alternating transverse rows on one face only of the zoarium. Jurassic to present day. Ex. *I. hagenowi*, Lower Greensand.

Entalophora. Zoarium of erect cylindrical branches, with the zoœcia opening on all sides of the branch and arranged irregularly or quincuncially. Jurassic to present day. Ex. *E. virgula*, Cretaceous.

Theonoa (=*Fascicularia*). Zoarium large, generally massive and globose. Zoœcia in the form of long tubes, with horizontal tabulæ, in contact laterally, and forming bundles which are either distinct and radiate from the base to the periphery, or fuse into laminæ which intersect. Jurassic to Pliocene. Ex. *T. aurantium*, Coralline Crag.

SUB-ORDER 2. TREPOSTOMATA

The zoœcia are calcareous, tubular, with transverse partitions, and of two sizes, the smaller apertures being known as *mesopores* and *acanthopores*; avicularia and vibracula are absent. The apertures of the zoœcia are round, polygonal, or irregular, and terminal and without opercula. Oœcia are absent. The Trepostomata are found chiefly in the Palæozoic formations, but a few genera linger on until the Cretaceous.

Monticulipora. Zoarium generally massive or lobate, covered with little raised portions called 'monticules.' Zoœcia polygonal, with thin walls. Ordovician and Silurian. Ex. *M. papillata*, Silurian.

SUB-ORDER 3. CRYPTOSTOMATA

The zoœcia are calcareous and tubular, often with transverse partitions, and often of two sizes. Avicularia and vibracula are absent. The external orifices of the zoœcia are round, but these are not the true apertures; the latter are situated at the bottom of a tubular vestibule, the round orifice of which is seen on the surface of the zoarium. Probably a chitinous operculum covered the true aperture, but it is never found in the fossils. Oœcia are absent. The Cryptostomata range from the Ordovician to the Permian.

Fenestella. Zoarium funnel-shaped or fan-shaped. Branches straight, united by cross-bars, so as to form a network. The cross-bars do not bear zoœcia. On each branch there is a median ridge or carina, on the sides of which the zoœcia occur. Openings of zoœcia round. Ordovician to Permian. Ex. *F. plebeia*, Carboniferous.

Rhabdomeson. Zoarium of cylindrical branches with an axial tube to which the proximal ends of the zoœcia are attached; the surface is divided into rhombic areas, arranged regularly, in the middle of which are the round orifices. Carboniferous. Ex. *R. rhombiferum*.

SUB-ORDER 4. CHEILOSTOMATA

The zoœcia are sometimes calcareous, sometimes horny, often both; they are more or less box-shaped, never tubular; and not divided by transverse partitions. Zoœcia, differing from the normal forms in size and shape, and modified for protective purposes, are often present, and are called avicularia and vibracula—according to whether their

function is to pinch or to sweep away foreign bodies which would settle on the zoarium. The apertures of the zoœcia are contracted and not terminal, of varying outline, and provided with a movable operculum, which being horny is not found in fossil specimens. Globular ovicells are often present; these are not modified individuals, but outgrowths in front of the distal end of each zoœcium. The Cheilostomata range from the Jurassic to the present day, but are rare in deposits earlier than the Chalk.

Membranipora. Zoarium encrusting or erect; the top of each zoœcium is covered with a chitinous membrane in which is situated the aperture; consequently in fossil specimens each zoœcium has a rim enclosing an unroofed space; the rim may have spines around it. Jurassic to present day. Ex. *M. elliptica*, Chalk.

Cribrilina. Zoarium usually encrusting. Zoœcia as in *Membranipora*, but the spines of the rim meet and fuse with their neighbouring and with their opposite fellows, and form an incomplete roof over the zoœcium. Tertiary and present day. Ex. *C. punctata*, Coralline Crag to Recent.

Pelmatopora. Like *Cribrilina*, but the costæ, or spines that form the front wall, are very coarse, and their broken upturned ends form a row or rows of hob-nail-like markings on each side of the mid-line of the front wall. Upper Cretaceous. Ex. *P. solearis*, Chalk.

Micropora. Zoarium encrusting. Zoœcia with an encircling rim as in *Membranipora*, but the chitinous roof is replaced by one of carbonate of lime; and this roof is perforated by two holes, one on each side, near the rim and proximally to the orifice. Cretaceous to present day. Ex. *M. cribriformis*, Barton Beds.

Cellepora. Zoœcia heaped irregularly upon an irregular encrusting or erect zoarium; the front wall entirely calcareous and very convex; the aperture terminal, more or less round, always accompanied by one or more small avicularia; in addition larger avicularia are often present between the normal zoœcia. Tertiary to present day. Ex. *C. tubigera*, Coralline Crag.

Distribution of the Polyzoa

By far the larger number of the Polyzoa are marine; they occur both in shallow and deep water. The deep-water forms belong mainly to the Cheilostomata; a few Ctenostomata occur at considerable depths, but the group is characteristic of shallow water. The Cyclostomata are comparatively rare at the present day, except in the Northern seas. The conditions under which the extinct Trepostomata and Cryptostomata flourished best are not known.

The earliest Polyzoa occur in the Ordovician rocks. Nearly all the Palæozoic genera are extinct; they belong mainly to the Trepostomata and Cryptostomata. The Cyclostomata are represented by a few genera in the Palæozoic rocks, and become increasingly abundant in the Mesozoic, attaining their maximum in the Upper Cretaceous. A few Cheilostomata have been recorded from the Jurassic rocks, but the group does not become abundant until the Cretaceous period; in the Tertiary it is better represented than the Cyclostomata. Very many of the Pliocene forms belong to species which are still living.

The chief genera found in the different systems are:—

Palæozoic. *Archimedes, Fenestella, Hemitrypa, Monticulipora, Pinnatopora, Polypora, Ptilodictya, Rhabdomeson, Thamniscus.*

Jurassic. *Berenicea, Ceriopora, Diastopora, Entalophora, Haploœcia, Idmonea, Proboscina, Spiropora, Stomatopora.*

Cretaceous. *Crisina, Diastopora, Entalophora, Heteropora, Lunulites, Membranipora, Onychocella, Pelmatopora, Proboscina, Stomatopora.*

Eocene. *Hornera, Idmonea, Membranipora.*

Pliocene. *Alveolaria, Cellepora, Cribrilina, Hornera, Lepralia, Membranipora, Theonoa*

PHYLUM MOLLUSCA

Classes.	*Sub-Classes.*	*Orders.*
1. Lamellibranchia.		
2. Gasteropoda	1. Isopleura.	
	2. Anisopleura	1. Streptoneura (Prosobranchia).
		2. Euthyneura.
3. Scaphopoda.		
	Orders.	*Sub-Orders.*
4. Cephalopoda	1. Tetrabranchia	1. Nautiloidea.
		2. Ammonoidea.
	2. Dibranchia	1. Decapoda.
		2. Octopoda.

THE majority of the molluscs (oysters, whelks, cuttlefish, etc.) are marine, but some live on land, others in fresh-water. Unlike the worms and arthropods, they are unsegmented animals, and they bear no serially repeated appendages. Typically the body is bilaterally symmetrical, and there is consequently a repetition of the same organs on each side; but in most gasteropods this symmetry is more or less completely lost. From the dorsal surface arises a fold of the skin forming what is known as the *mantle*; this generally secretes a calcareous shell, consisting of one or two (occasionally more) pieces. On the ventral surface of the body is the *foot*—a muscular organ used in locomotion. In most cases respiration takes place by means of gills, which are placed in the cavity enclosed by the

mantle. A heart is present, and is placed on the dorsal surface; it consists usually of a ventricle and two auricles. The mouth is situated anteriorly, and, except in the lamellibranchs, is provided with a rasping organ, the *odontophore*; the anus, in typical forms, is placed posteriorly. Renal organs (nephridia) are present and place part of the body-cavity in communication with the exterior. The nervous system consists of a ring round the œsophagus, and usually of three main groups of ganglia, from which nerves are given off. Only sexual reproduction occurs; most forms are unisexual, a few hermaphrodite.

The Mollusca are divided into four classes:—(1) Lamellibranchia, (2) Gasteropoda, (3) Scaphopoda, (4) Cephalopoda.

CLASS I. LAMELLIBRANCHIA

In the lamellibranch, as in the brachiopod, the shell is generally calcareous and consists of two valves, but these instead of being dorsal and ventral as in the latter, are placed one on the right, the other on the left side of the body, and the two are joined together by means of a hinge and a ligament at the dorsal margin. The interior of the shell is lined by a fold of the skin, the *mantle* (fig. 104, *m*), which is divided into two lobes, one being placed in each valve. In the middle of the space enclosed by the mantle (the mantle-cavity) and projecting from the ventral surface of the visceral mass, is the foot (*f*). This is a laterally flattened muscular organ, frequently hatchet-[1] or ploughshare-shaped, and is used for crawling, or for burrowing in sand or mud. Sometimes, as in the case of *Trigonia*, by means of a rapid movement it enables the animal to jump to a considerable distance. In the genus

[1] Hence the name *Pelecypoda* used by some authors for this class.

Mytilus the foot is very much reduced; in others which have lost the power of locomotion (*e.g. Ostrea*) it is absent altogether. On the posterior part of the foot there is in some genera (*e.g. Mytilus, Pinna, Arca*) a gland which

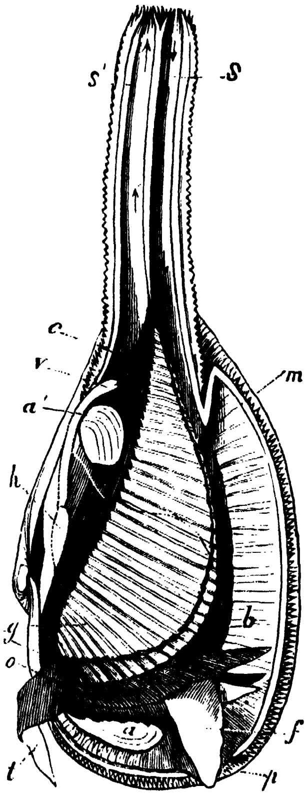


Fig. 104. *Mya arenaria*. The left valve and mantle and half the siphons have been removed. *a*, anterior adductor muscle; *a'*, posterior adductor; *b*, visceral mass; *c*, cloacal chamber into which the anus opens; *f*, foot; *g*, branchiæ; *h*, heart; *m*, cut edge of the mantle; *o*, mouth; *p*, edge of mantle; *s*, branchial siphon; *s'*, anal siphon; *t*, labial palps; *v*, anus. (From Woodward.)

secretes a bundle of horny fibres, known as the *byssus*, by means of which the animal moors itself to foreign objects. On each side of the foot, between it and the mantle, and attached to the body dorsally, are the gills or branchiæ (fig. 104, *g*); these consist of filaments which usually become connected so as to form leaf- or plate-like bodies, whence the name Lamellibranchia.

In some forms the margins of the two mantle-lobes although in contact are not united, and when this is the case there are usually at the posterior margin two openings leading from the exterior to the mantle-cavity; these are produced by adjoining excavations or notches in the two lobes of the mantle. A current of water, caused by the cilia on the gills and mantle, flows in through the ventral opening, and provides the animal with food and oxygen; another current flows out through the dorsal opening, carrying with it fæcal matters. In many cases, however, the two lobes of the mantle are fused at one or more points; this union occurs between the exhalent and inhalent openings, and also, in many forms, below the latter opening. In this way the mantle becomes a kind of bag, having three openings, a ventral for the protrusion of the foot, and two posterior for the inhalent and exhalent currents of water. Frequently, at the posterior openings, the mantle is greatly produced so as to form two complete tubes, known as *siphons* (fig. 104, *s*, *s′*); these are sometimes free, sometimes united, and may be as much as four times the length of the shell. The ventral is generally the longer; it is furnished with tactile papillæ, and is known as the *branchial siphon* (*s*), the dorsal being the *anal siphon* (*s′*). In many forms the siphons can be withdrawn into the shell by means of muscles. Occasionally, as in *Teredo* the siphons are surrounded by a calcareous tube.

The shell can be closed by means of the adductor muscles (a, a'), which pass from the interior of one valve to the other. In many genera there are two adductors, and these forms are frequently spoken of as the *Dimyaria*; others, known as the *Monomyaria*, possess one adductor only, and when this is the case it is the posterior which is present, the anterior having atrophied; this occurs in the oyster, but in this, and in all other forms so far as is known, the anterior muscle is present in the young state.

In the lamellibranchs there is no head, hence the class is sometimes spoken of as the *Acephala*. The mouth (o) is in the middle line of the body, ventral to the anterior adductor muscle, and is not provided with organs of mastication. At each side are two leaf-like processes, the *labial palps* (t). The mouth leads into a short œsophagus, which passes into a globular stomach surrounded by the liver; next is the intestine, which, after undergoing many convolutions in the foot, reaches the dorsal surface of the body, where it passes through the pericardium and is surrounded by the ventricle of the heart. The anus (v) is situated dorsally to the posterior adductor muscle. The nervous system usually consists of three pairs of ganglia. One pair is placed at the sides of the mouth and is connected by nerve-cords with a pair in the foot, and with a third pair placed beneath the posterior adductor muscle. From these ganglia nerves are given off to the muscles, gills, etc. Tactile organs are present on the margin of the mantle and especially on the ventral siphon. In some forms eyes occur at the ventral margin of the mantle-lobes; they are especially well-developed in the genus *Pecten*. The heart (h) is placed dorsally, just below the hinge, and is surrounded by a large pericardial cavity; it consists of two auricles, and a ventricle, which, as already mentioned,

extends round the intestine. The renal organs consist of a pair of glandular tubes underneath the pericardium. In almost all cases the sexes are separate, but a few forms are hermaphrodite.

As already mentioned, the two valves of the shell are on the sides of the animal. The margin near the hinge (fig. 105, B, *d—l*) is dorsal, the opposite (*v*), where the valves open, is ventral; that near the mouth is anterior (*a*), that near the anus and siphons posterior (*p*). In the majority of cases the two halves are equal or almost equal

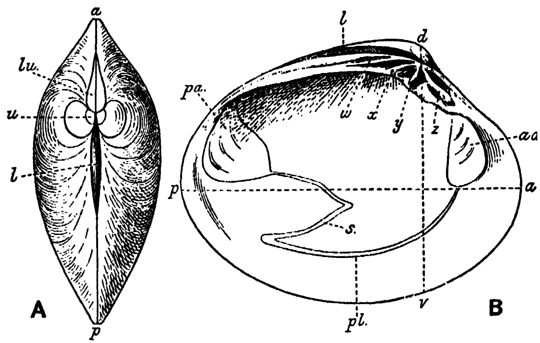


Fig. 105 *Meretrix* (*Callista*) *chione*, Recent. A. Dorsal view of the two valves. B. Interior of left valve. × ½. *a*, anterior border; *p*, posterior; *d*, dorsal; *v*, ventral; *lu*, lunule; *u*, umbo; *l*, ligament; *aa*, anterior adductor impression; *pa*, posterior adductor; *pl*, pallial line; *s*, pallial sinus; *w*, *x*, *y*, cardinal teeth; *z*, anterior lateral tooth.

in size, and each valve is generally inequilateral. But in some (*e.g. Pectunculus*) the shell is nearly equilateral, and in others (*e.g. Ostrea*) it is inequivalve. When the shell is equilateral the direction of greatest growth is perpendicular to the hinge-line; when inequilateral the direction is oblique to the hinge-line. Each valve may be regarded as a greatly depressed hollow cone, the apex of which forms the *umbo* (fig. 105 A, *u*); these umbones are sometimes

straight (*e.g. Pecten*), but generally curved towards the anterior margin; in a few genera (*e.g. Nucula, Trigonia, Exogyra*) they are directed posteriorly; in *Diceras* they are spiral. Sometimes there is in front of the umbones, and bounded by a groove, an oval depressed area (*lu*), half being on each valve; this is termed the *lunule*. Behind the umbones there is sometimes a somewhat similar, but larger area, known as the *escutcheon*.

In the interior of the valves various markings, produced by the union of the muscles with the shell, may be noticed (fig. 105 B). The adductors form oval, round, or sometimes elongated depressions (the *adductor impressions, aa, pa*); in the Dimyaria there are two in each valve, one being near the anterior border, the other near the posterior; in the Monomyaria the single adductor impression is usually near the middle of the valve. When, as in the genus *Mya*, the two muscles are placed at equal distances from the hinge-margin, they are of nearly the same size, since on account of their position they are equally efficient in closing the valves; but in forms like *Mytilus*, where the shell is very inequilateral and the anterior muscle is close to the umbo but the posterior at a considerable distance from it, the latter is much larger than the former, since it is placed in a more advantageous position for closing the valves. For the same reason the single muscle of the Monomyaria is attached near the centre of the valves. Less important than the adductor impressions are those produced by the muscles for the movement of the foot (protractors and retractors); these occur close to the anterior and posterior adductors. Passing from one adductor impression to the other in each valve is a linear depression, caused by the attachment of the muscles of the mantle to the shell, and known as the *pallial line* (*pl*). In some forms this line runs

evenly between the two adductor impressions and parallel with the margin of the valve; it is then said to be *simple* or *entire*. But in those genera which possess retractile siphons the pallial line bends inward just before reaching the posterior adductor; this indentation is known as the *pallial sinus* (*s*), and is caused by bending inwards of the part of the pallial muscles which serve for the retraction of the siphons.

The hinge is formed by projections known as teeth, which alternate in the two valves, the teeth of one valve fitting into the depressions between those of the other. The margin of the valve on which the teeth occur is known as the *hinge-line*; generally it is curved, but in some genera it is straight (*e.g. Arca*). Several types of hinge may be recognised:—(1) *Taxodont:* the teeth are numerous and more or less similar in form and size, *e.g. Nucula* (fig. 106 A). (2) *Dysodont:* the teeth are of a simple type, and are developed from internal ribs at the margin of the valve; the hinge-margin may be simple or somewhat thickened, *e.g. Mytilus.* (3) *Isodont:* there are two strong teeth of equal size in each valve, which fit into corresponding sockets in the other valve; between the teeth is a median ligament-pit, *e.g. Spondylus* (fig. 106 D, E). (4) *Schizodont:* the teeth are few in number, thick, and sometimes grooved; the middle tooth in the left valve is often bifid, *e.g. Trigonia* (fig. 106 B, C). (5) *Heterodont:* the teeth are few in number and not all of uniform shape and size; some (usually two or three) are placed immediately under the umbo and are known as the *cardinal* teeth, others, termed *laterals,* are placed in front of and behind the umbo, forming the *anterior* and *posterior laterals*; some or all of the cardinals or of the laterals may be absent; the hinge-margin is usually extended as a vertical lamina or *hinge-*

plate (fig. 106 F) on which the teeth are borne, *e.g. Meretrix*. (6) *Desmodont:* true teeth and a hinge-plate are absent, but one or more laminæ or ridges are developed at the hinge-margin, *e.g. Pleuromya*. (7) In some genera teeth are absent; this may be a primitive character, as in

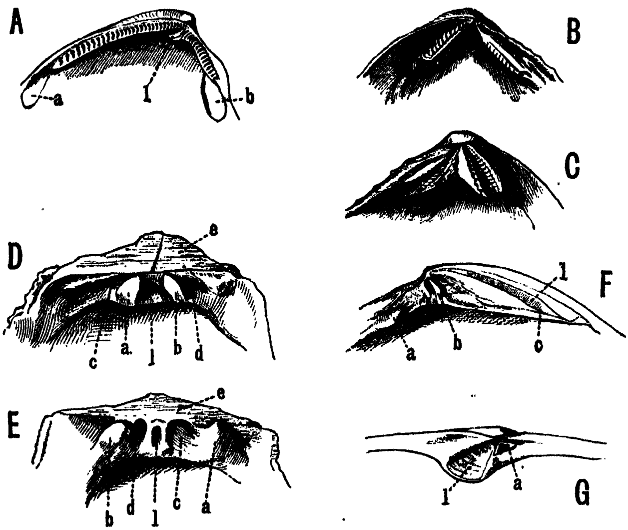


Fig. 106. Some types of hinge. A. *Nucula*. *a*, anterior adductor; *b*, posterior adductor; *l*, ligament-pit. B, C. *Trigonia*. B, right valve with two large striated teeth; C, left valve with three teeth. D, E. *Spondylus*. D, right valve; E, left valve. *a*, *b*, teeth; *c*, *d*, sockets into which the teeth fit; *e*, area; *l*, ligament-pit. F. *Lucina* (right valve). *a*, anterior lateral tooth; *b*, cardinal tooth; *c*, posterior lateral tooth; *l*, ligament. G. *Lutraria* (left valve). *a*, strong Λ-shaped cardinal tooth; *l*, process to which the ligament is attached. All drawn from recent specimens.

Grammysia, or the result of degeneration as in *Ostrea* and *Anodonta*.

In some genera (*e.g. Arca*) there is, between the hinge-line and the umbo of each valve, a flattened triangular part of the shell, known as the *area* (fig. 106 D, *e*); when

this is present the umbones of the two valves are of course widely separated. The lunule and escutcheon (p. 215) appear to represent the anterior and posterior parts of the area. Some lamellibranchs (*e.g. Pecten*) have, on each side of the umbo, triangular or wing-like extensions of the shell, known as *ears.*

In the brachiopods the valves are opened by divaricator muscles, but in the lamellibranchs the work of these muscles is performed by the ligament. This consists of two parts, the external (fig. 105, *l*), and the internal (sometimes erroneously termed the cartilage) (fig. 106 G, *l*). One or other may be absent. The *external ligament* is composed of horny material; it is placed at the hinge-margin, usually posterior to the umbones, and is frequently attached to more or less prominent ridges; in some genera (*Pectunculus*) the external ligament extends both in front of and behind the umbones. The *internal ligament* consists of parallel elastic fibres, and is placed in grooves or sockets along the hinge, so that when the valves are closed it is compressed, and, being elastic, tends to force the valves apart—its action is similar to that of a piece of indiarubber placed in the hinge-line of a door. The external ligament acts like a C-spring, and is bent when the valves are closed. Consequently, in order to open the shell, the animal has merely to relax its adductor muscles. Occasionally the ligament is preserved in fossil specimens.

The *length* of a lamellibranch shell is measured from the anterior to the posterior margin (fig. 105 B, *a*—*p*), the *breadth* or *height* from the umbo to the ventral margin (*d*—*v*), the *thickness* from one valve to the other at right angles to the lines of length and breadth.

The shell is secreted by the mantle; its structure varies in different groups. In some genera it consists of two

calcareous layers; the inner is the *pearly* or *nacreous* layer, and is formed of numerous thin lamellæ (fig. 107 *a*); the

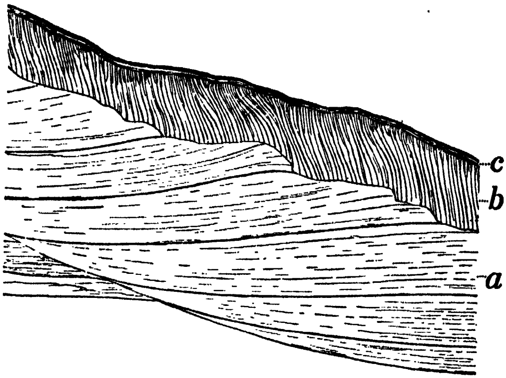


Fig. 107. Vertical section of the shell of a recent *Unio*, cut in a radial direction from the umbo; the right-hand side of the section is near the ventral margin. *a*, pearly or nacreous layer, in which the later lamellæ overlap the earlier and extend on to (*b*) the prismatic layer; *c*, periostracum. × 10.

outer is the *prismatic* layer (figs. 107 *b*, 108), and is composed of prisms placed more or less nearly perpendicular to the surface of the shell, each prism being encased in a thin membranous sheath, which can be isolated by dissolving the calcareous part of the shell in acid. The external surface is covered by a green or brownish horny layer (*c*), the *periostracum* (frequently referred to as the 'epidermis'). The prismatic layer is formed by the margin of the mantle only; the pearly layer by the general surface of the mantle, and this

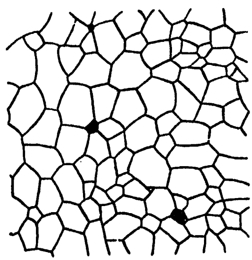


Fig. 108. Section of prismatic layer of recent *Pinna*, parallel to the surface of the shell and at right angles to the prisms. Magnified.

layer gradually encroaches on the former, which consequently cannot afterwards increase in thickness, whereas the pearly layer may do so throughout the life of the animal. The pearly layer is absent in many forms, and the prismatic structure of the outer layer may be indistinct or altogether wanting, and this layer has then a porcellanous appearance. Sometimes the shell consists entirely of aragonite or of calcite; in other cases one layer may be of calcite and the other of aragonite.

The surface of the shell may be smooth, or may be ornamented with radiating or concentric ribs and striæ, or with tubercles, or spines. Often the exterior shows concentric lamellæ, which represent periods of growth. The part of the shell at the umbo is that which was first formed, and often differs in ornamentation and form from the other parts. The margins of the valves may be smooth or crenulated; sometimes, as in some species of *Pecten*, the entire shell is corrugated, thus increasing its strength without materially adding to the weight. In many genera the two valves can be completely closed, in others they are always open at some part, and are then said to be *gaping*; this gape occurs most frequently at the posterior end, but sometimes also anteriorly. Sometimes the small embryonic shell, known as the *prodissoconch*, is found at the umbo of the adult shell; this represents the protegulum of the Brachiopods (p. 180) and the protoconch of the Gasteropods and Cephalopods.

In order to be able to distinguish the right and left valves we must determine first the anterior and posterior margins. When the soft parts of the animal are present this is easily done; but when the shell only is before the observer the points to be noticed are the following:—

(1) The umbones are generally directed anteriorly;

and in inequilateral shells, the posterior part of the valves is, with only a few exceptions (*Nucula*, *Lima*), longer than the anterior part.

(2) The lunule is anterior to the umbones.

(3) The external ligament is commonly posterior to the umbones, and is never entirely in front of them.

(4) The pallial sinus is posterior.

(5) When one adductor impression only is present, it is the posterior.

(6) When one adductor impression is distinctly larger than the other, the larger is the posterior.

Having found the anterior and posterior margins, the shell should be placed with the dorsal surface uppermost and the anterior margin pointing away from the observer, then the right and left valves will be on his right- and left-hand sides respectively.

Most of the lamellibranchs are free, but a few forms, such as the oyster, are permanently attached by one valve, which has been secreted by the mantle directly on to a rock or some other object to which it adheres firmly. In some cases the right valve is fixed, in others the left. The shell in these forms becomes irregular and the fixed valve is larger and thicker than the free valve. Other genera are attached by means of a byssus (p. 212), which often passes out through a notch or sinus in the margin of one or both valves—such forms tend to become inequilateral. In the free forms, movement takes place usually by means of the foot, but some genera (*Pecten*, *Lima*) move by the rapid opening and shutting of the valves. A few are capable of making borings into various substances; thus *Teredo*, the ship-worm, bores into wood, *Lithodomus* and *Saxicava*

into limestone, and *Pholas* into various materials, such as sandstone, limestone, gneiss, peat, and amber. Wood perforated by *Teredo* has been found fossil in various formations of Eocene and Oligocene age.

The features which more especially characterise the lamellibranchs as a class are: the absence of a head and of organs of mastication, the bilateral symmetry, the division of the mantle into two lobes, the bivalve shell and the lamellar gills. Although at first sight the shell appears to resemble closely that of the brachiopods, it differs in several important respects:—(1) the valves are right and left, instead of dorsal and ventral, (2) they are generally inequilateral and equivalve, (3) teeth occur on both valves, (4) a ligament is present, (5) the umbones are never perforated for a peduncle, (6) the microscopic structure of the shell is different.

Various classifications of the Lamellibranchia have been, from time to time, proposed. By Lamarck this class was divided into the *Monomyaria* and the *Dimyaria*, depending on the presence of *one* or *two* adductor muscles. Between these two groups, however, there are numerous intermediate forms in which the anterior muscle is smaller than the posterior; and, further, one genus (*Dimya*), which in other respect agrees with some of the Monomyaria possesses two adductor muscles. A third division, the *Heteromyaria*, was established for the genera in which the anterior adductor is small, but its limits are not well defined, and moreover, in *Mytilus* it is found that whilst in *M. edulis* both muscles are present, in the closely allied species, *M. latus*, the anterior adductor is absent. Another classification, which was suggested by Fleming, was based on the presence or absence of siphons; the two groups being termed the *Siphonida* and the *Asiphonida*; the former

has been further divided according as to whether the pallial line is entire (*Integripalliata*) or provided with a sinus (*Sinupalliata*). Neumayr, Dall, and others have divided the lamellibranchs into groups based largely on the character of the hinge (p .216); whilst the classification brought forward by Pelseneer, is founded on the form and structure of the gills. The divisions which are provisionally used in the following pages are similar to those proposed by Neumayr.

1. Hinge taxodont. Two nearly equal adductor muscles. Siphons usually wanting.

Nucula[1] (fig. 106 A). Shell equivalve, trigonal or oval, closed, posterior side very short; umbones directed posteriorly. Surface smooth or ornamented. Interior nacreous. Margins of valves smooth or crenulated. Hinge angular, with a median internal triangular ligament-pit, and numerous sharp teeth. Adductor impressions nearly equal. Pallial line simple. Silurian to present day. Ex. *N. hammeri*, Lias; *N. dixoni*, Bracklesham Beds.

Nuculana (=*Leda*). Similar to *Nucula*. Posteriorly the shell is produced and pointed, and provided with a ridge or carina. Pallial line with a small sinus. Margins smooth. Lunule lanceolate. Silurian to present day. Ex. *N. lachryma*, Inferior Oolite to Cornbrash; *N. caudata*, Pliocene to present day.

Ctenodonta. Shell oval or elongated, nearly equilateral, smooth or with concentric striæ. Ligament external. No area. Hinge curved or angular, with numerous small teeth. No internal ligament-pit. Pallial line simple. Cambrian to Carboniferous. Ex. *C. pectunculoides*, Ordovician.

Arca. Shell thick, generally equivalve, sub-quadrangular, ventricose, ornamented with radiating ribs and concentric striæ; margins smooth or dentate; closed or gaping ventrally. Hinge straight, with numerous, small, equal, transverse teeth. Umbones prominent, separated by the large areas, which have numerous ligamental grooves converging from the hinge-margins to the umbones. Adductor

[1] All the genera of Mollusca described are marine unless otherwise stated.

impressions sub-equal, the anterior rounded, the posterior divided. Pallial line simple. Jurassic to present day. Ex. *A. tetragona*, Pliocene to present day; *A. granosa*, Recent.

Cucullæa. Shell similar to *Arca*; ventricose, sub-equilateral, valves closed. Hinge with short central transverse teeth, and two to five lateral teeth nearly parallel to the hinge-margin. Posterior adductor fixed to a thin raised plate. Jurassic to present day. Wide-spread in the Mesozoic. Living in the Indian Ocean and China Sea. Ex. *C. fibrosa*, Upper Greensand.

Pectunculus (= *Glycimeris*, *Axinæa*). Shell thick, solid, sub-orbicular, equivalve, almost equilateral. Surface smooth or radially striated. Ligament external, on the area. Umbones central, slightly curved posteriorly; a small triangular area provided with diverging grooves for the ligament. Hinge arched or semicircular, with a row of numerous, small, strong, transverse teeth, obliterated at the centre in the older forms by the growth of the area. Margins crenulate inside; adductor impressions sub-equal—the anterior sub-triangular, the posterior oval or rounded. Pallial line with a very small sinus. Cretaceous to present day. Ex. *P. glycimeris*, Pliocene to present day.

2. Hinge dysodont, but teeth sometimes rudimentary or absent. Anterior adductor smaller than the posterior, sometimes absent in the adult. Pallial line simple.

Mytilus. Shell thin, equivalve, very inequilateral, elongated, sub-triangular, posterior border rounded; with a small gape for the well-developed byssus. Umbones sharp, terminal, anterior. Teeth small or absent. Ligament linear, marginal, sub-internal. Anterior adductor impression small, placed near the umbo; posterior large; pallial line simple. Trias to present day. Ex. *M. edulis*, Pliocene to present day.

Modiola. Shell similar to *Mytilus*, but oblong, inflated in front. Umbones obtuse, anterior, but not terminal. Devonian to present day. Ex. *M. modiola*, Recent; *M. imbricata*, Inferior Oolite.

Lithodomus (= *Lithophagus*). Shell similar to *Modiola*; sub-cylindrical, rounded in front, wedge-like behind. *Lithodomus* bores into limestone, etc. Carboniferous to present day. Ex. *L. inclusus*, Inferior Oolite to Corallian.

Modiolopsis. Shell thin, smooth, elongate, very inequilateral, anterior part small, posterior part enlarged. Umbones nearly terminal, close together; a depression crosses the valves obliquely from the umbo. No teeth. Anterior adductor impression deep; posterior adductor large, faintly marked. Ordovician and Silurian. Ex. *M. modiolaris*, Ordovician.

Myoconcha. Similar to *Modiolopsis*, but usually with a long cardinal and a long slender posterior lateral tooth in the right valve. Carboniferous to Chalk. Ex. *M. crassa*, Inferior Oolite; *M. cretacea*, Chalk.

Hippopodium. Shell very thick, very convex, oblong; surface with lines of growth. Umbones large, anterior. Hinge thick, with one oblique tooth which may disappear in old specimens. Adductor impressions deep. Pallial line simple. Lias to Great Oolite. Ex. *H. ponderosum*, Lower and Middle Lias.

Myalina. Shell thick, trigonal, oblique, very inequilateral, with pointed umbones at the anterior extremity. Anterior marginal part of valves sharply bent. Posterior part compressed, wing-like. Hinge-line straight, long. Hinge-margin broad with longitudinal striations. Anterior adductor near the ventral edge of the anterior end of the hinge-plate. Posterior adductor large, oval. Pallial line simple. Surface with growth-lines, often lamellar. Silurian to Permian; common in Carboniferous. Ex. *M. verneuili*, Carboniferous.

Pinna. Shell generally thin, with coarse prismatic structure (fig. 108), equivalve, inequilateral, wedge-shaped, without ears. Umbones sharp, anterior, terminal. Valves truncate and gaping posteriorly. Hinge-line straight, long. No teeth. Ligament linear, almost entirely internal, lodged in a groove. Posterior adductor large, sub-central; anterior adductor close to the umbo. Carboniferous to present day. Ex. *P. hartmanni*, Lias; *P. affinis*, London Clay.

Gervillia. Shell obliquely elongated, very inequilateral, slightly inequivalve, the left valve a little more convex than the right; umbones almost terminal. Hinge straight, with broad margin on which are numerous perpendicular, widely-separated ligament-pits; with two or more oblique ridge-like teeth. Ears indistinctly limited from

the rest of the shell, the anterior very short, the posterior long. Posterior adductor impression large, sub-central. Trias to Eocene. Ex. *G. Forbesiana*, Gault; *G. sublanceolata*, Lower Greensand.

Inoceramus. Shell variable in form, circular, oval, or oblong; inequilateral, inequivalve, ventricose or compressed, with ears indistinctly limited. Umbones prominent, rather anterior. No teeth. Surface with concentric (or rarely radiating) furrows. Hinge-line straight, usually long, with numerous parallel, close-set, transverse ligament-pits. Adductor impression rarely visible. Inner layer of shell thin and nacreous; outer layer thick, formed of large prisms. Lias to Chalk; common in Upper Cretaceous. Ex. *I. concentricus*, Gault; *I. brongniarti*, Chalk.

Perna. Shell nearly equivalve, inequilateral, compressed, subquadrate or sub-circular. Umbones at the anterior end. Hinge-line straight, without teeth; hinge-margin broad, with numerous transverse, elongated ligament-pits placed close together and parallel with one another. Right valve with a byssal sinus. Adductor impression large, sub-central, double; pallial line simple. Posterior ear often large, not distinctly limited. Trias to present day. Ex. *P. mytiloides*, Upper Jurassic; *P. ephippium*, Recent.

Pteria (= *Avicula*). Shell oblique, inequilateral, inequivalve, left valve more convex than the right. Interior nacreous. Hinge long, straight, with one or two small cardinal teeth and a lamellar lateral tooth. Posterior ear wing-like and longer than the anterior. A byssal sinus under the right anterior ear. Area small. Ligament long, partly internal, partly external, in a groove. Posterior adductor impression large, sub-central. Trias to present day. Ex. *P. media*, Barton Beds; *P. hirundo*, Recent. Sub-genera or closely allied genera, are *Actinopteria*, *Leiopteria*, *Pteronites* (all Upper Palæozoic), and *Oxytoma* (Mesozoic).

Pseudomonotis. Similar to *Pteria*, but the shell is oval, the left valve large and very convex, and the right valve flattened; the anterior ear small or rudimentary. Carboniferous to Cretaceous. Ex. *P. echinata*, Cornbrash.

Aucella. Shell thin, obliquely elongate, inequilateral, inequivalve, with concentric folds or ribs. Left valve convex, with prominent incurved umbo; ears indistinctly limited. Right valve flattened, anterior ear triangular, with a deep byssal sinus; posterior

ear indistinctly limited. Hinge-line straight, short, without teeth. Ligament external. Upper Jurassic and Lower Cretaceous. Ex. *A. keyserlingi*, Speeton Series.

Pterinea. Form similar to *Pteria*; left valve flattened. Hinge with small transverse anterior teeth, and laminar posterior teeth. Area large, with longitudinal grooves for the ligament. Posterior adductor impression large, shallow; anterior impression small, deep, below the anterior ear. Ordovician to Carboniferous; common in Devonian. Ex. *P. lævis*, Devonian.

Posidonomya. Shell thin, oblique, oval, equivalve, compressed, with concentric furrows. Umbones small, sub-central. Hinge-line straight, short, without teeth; posterior ear compressed, indistinctly limited. Silurian to Jurassic. Ex. *P. becheri*, Carboniferous.

Conocardium. Shell more or less trigonal, very inequilateral, with radiating ribs; posterior side short, truncated, forming a cordate posterior end, produced into a long tube; anterior side oblique, compressed, wing-like, gaping. Umbones small, pointed, incurved. Hinge-line long, straight. Ligament partly external, partly internal, attached to a plate behind the umbones. Anterior adductor impression large, deep; posterior impression shallow. Inner margins of valves toothed. The truncated end bearing the tube is regarded by some authors as anterior, and the wing-like end as posterior. The affinities of this genus have not yet been determined. Silurian to Carboniferous. Ex. *C. hibernicum*, Carboniferous Limestone.

3. Hinge, when well-developed, isodont; teeth sometimes absent or imperfect. A median pit for the ligament. Siphons absent. Posterior adductor only present.

Spondylus (fig. 106 D, E). Shell irregular, with ears, attached by the right valve; surface with radiating ribs which are spiny or foliaceous. Right valve larger and more convex than the left, with a triangular area. Two strong teeth in each valve, which fit into corresponding sockets in the other valve; between the teeth a triangular ligament-pit; ligament partly external. Adductor impression large, sub-central. Jurassic to present day. Living in

warm seas. Ex. *S. spinosus*, Chalk; *S. rarispina*, Bracklesham; *S. gæderopus*, Recent.

Plicatula. Similar to *Spondylus*. Surface smooth, folded or scaly. Without ears. Area very small. Ligament internal. Adductor impression excentric. Trias to present day. Living mainly in warm seas. Ex. *P. spinosa*, Lias; *P. inflata*, Chalk; *P. cristata*, Recent.

Anomia. Shell thin, irregular or sub-circular, attached by a calcified byssus, which passes through a rounded sinus near the umbo of the right valve. Right valve flattened, with a central adductor impression; left valve larger, convex, with three impressions of the byssal muscles and one of the adductor. Teeth absent. Lias to present day. Ex. *A. ephippium*, Pliocene to present day.

Pecten. Shell sub-circular, ovate or trigonal, closed, almost equilateral, inequivalve or nearly equivalve. Surface frequently with radiating ribs or striæ, sometimes smooth or with concentric ridges. Hinge-line straight; with well-developed ears, with or without a byssal sinus. A central, triangular pit for the internal ligament. Adductor impression large, a little excentric. Carboniferous to present day. *Pecten* includes a very large number of species, which are grouped into sub-genera and sections, of which the more important are: *Æquipecten* (ex. *Pecten asper*, Upper Greensand, *P. opercularis*, Pliocene); *Amusium* (ex. *P. pleuronectes*, Recent); *Camptonectes* (ex. *P. lens*, Jurassic); *Chlamys*, *Hinnites*, *Neithea* (see below); *Syncyclonema* (ex. *P. orbicularis*, Chalk).

Chlamys: shell ovate or trigonal, nearly equivalve, surface with radial ribs. Ears large—the anterior larger than the posterior and with a deep sinus for the byssus on the right valve. Trias to present day. Ex. *P. islandicus*, Pleistocene and Recent.

Hinnites: the young shell is like *Chlamys*; the adult is irregular like *Ostrea*, and is attached by the right valve. Cretaceous to present day. Ex. *H. cortesi*, Pliocene.

Pecten (restricted): right valve very convex, left flattened. Ears nearly equal. No byssal sinus. Cretaceous to present day. Ex. *P. maximus*, Pliocene to present day.

Neithea: similar to the last; with numerous small denticles on the hinge. Cretaceous. Ex. *P.* (*Neithea*) *quadricostatus*, Upper Greensand.

Lima. Shell obliquely oval, anterior part larger than the posterior part, equivalve, compressed, with radiating striæ or ribs. Valves gaping anteriorly and sometimes posteriorly. Umbones distant, sharp. Hinge-line straight without teeth, with unequal ears. On each valve a triangular area, with a central ligament-pit. Adductor impression large. Two small pedal impressions. Carboniferous to present day. Ex. *L. gigantea*, Lias; *L. cardiiformis*, Middle Jurassic; *L. squamosa*, Recent. Sub-genera *Plagiostoma* (*L. gigantea*, Lias), *Limatula* (*L. fittoni*, Upper Greensand), *Mantellum* (*L. hians*, Recent), etc.

Aviculopecten. Shell ovate, slightly inequilateral; right valve less convex than the left. Umbones distinct; hinge-line straight, long; ears distinctly limited, the posterior larger than the anterior and often wing-like; a byssal sinus beneath the anterior ear in the right valve. Hinge-margin with narrow, nearly parallel grooves. A central pit for the internal ligament. Adductor impression large, sub-central. Surface usually with radial ribs, and concentric lines, the ornamentation different on the two valves. Devonian to Permian. Ex. *A. tabulatus*, Carboniferous.

Pterinopecten. Similar to *Aviculopecten*; posterior ear not distinctly limited; both valves with the same kind of ornamentation. Devonian and Carboniferous. Ex. *P. papyraceus*, Carboniferous.

Ostrea. Shell with lamellar structure, irregular, inequivalve, slightly inequilateral, fixed by the left (larger) valve. Left valve convex, often with radiating ribs or striæ; umbo prominent, sometimes directed anteriorly, sometimes posteriorly. Right valve flat or concave, often smooth. Ligamental cavity triangular or elongated. Hinge without teeth. Adductor impression sub-central; pallial line indistinct. Trias to present day. Ex. *O. deltoidea*, Kimeridgian; *O. edulis*, Pliocene and Recent.

Alectryonia. Includes the forms of *Ostrea* in which both valves have coarse angular folds; edges of valves toothed. The forms included in *Alectryonia* are polyphyletic. Trias to present day. Ex. *A. gregaria*, Corallian: *A. diluviana* (=*frons*), Chalk.

Gryphæa. Shell similar to *Ostrea*, but fixed in the young stage only, free in the adult; left valve large and convex, with a prominent incurved umbo. Right valve flattened or concave. Lias. Ex. *G.*

arcuata (=*incurva*), Lias. (In later formations *Gryphæa*-like forms have originated independently from more than one species of *Ostrea.*)

Exogyra. Similar to *Ostrea.* Shell fixed by the left (larger) valve. Right valve flat, resembling an operculum. Umbones more or less spiral, directed posteriorly. Upper Jurassic to Chalk. Ex. *E. columba*, Upper Greensand.

4. Hinge schizodont, or formed of thick, irregular teeth. Valves equal. Two nearly equal adductors. Ligament usually external and behind the umbones. Pallial line simple. Inner layer of shell usually pearly.

Trigonia (fig. 106 B, C). Shell thick, usually ornamented with concentric rows of tubercles or with concentric (sometimes radiating) ribs; trigonal, very inequilateral, anterior margin rounded, posterior produced and angular. Generally with a ridge extending from the umbones to the posterior border, cutting off a portion which has a different ornamentation. Umbones anterior, directed posteriorly. Cardinal teeth diverging, grooved, two in the right valve, three in the left, the central tooth in the latter being bifid. Ligament marginal, thick. Adductor impressions deep, the anterior smaller than the posterior, and placed near the umbones. A pedal impression in front of the posterior adductor of each valve and also one in the umbo of the left valve. Pallial line simple. Interior of shell nacreous. Lias to present day; abundant and widely distributed in the Jurassic and Cretaceous; found in the Australian region in the Tertiary and at the present day. Ex. *T. costata*, Inferior Oolite to Cornbrash; *T. clavellata*, Corallian.

Schizodus. Similar in form to *Trigonia*; shell thin and smooth, umbones placed anteriorly. Three teeth in each valve, the middle one being a cardinal; the anterior lateral inconspicuous in the right valve. Adductor impressions shallow. Carboniferous and Permian. Ex. *S. obscurus*, Permian.

Myophoria. Allied to *Schizodus.* Shell oval, triangular, or trapezoidal. Umbones anterior, often with a ridge extending to the lower part of the posterior border. Surface nearly smooth or with radial ribs. Right valve with one, sometimes two, cardinal teeth, and ridge-like posterior lateral tooth. Left valve with a triangular, sometimes bifid cardinal, and one anterior and one posterior lateral tooth.

Adductor impressions with a ridge passing to the hinge. Trias and Rhætic. Ex. *M. lævigata*, Trias.

Unio. Shell thick, oval or elongated, with a thin periostracum. Surface smooth, tuberculate, striated, or folded; interior nacreous. Umbones more or less anterior, often corroded. Ligament external, elongated. In the right valve one or two thick, irregular teeth below the umbo, and a long lamellar posterior lateral tooth; in the left valve, two thick irregular teeth near the umbo, and two long lamellar posterior lateral teeth. Adductor impressions very deep, especially the anterior. Pallial line simple. Inferior Oolite to present day. Lives in fresh water. Ex. *U. littoralis*, Pleistocene and Recent.

Anodonta. Allied to *Unio*; shell relatively thin, without teeth. Fresh water. Miocene (perhaps Purbeck) to present day.

Carbonicola (= *Anthracosia*). Similar in form to *Unio*, but the anterior part of shell is broad and tumid, the posterior part narrow and compressed; usually a constriction at the ventral border. Hinge-plate triangular, with or without cardinal teeth, no laterals. Ligament external. Adductors large, the anterior near the margin. Pedal impression above the anterior adductor. Pallial line simple. Carboniferous and Permian. Probably fresh water. Ex. *C. robusta*, Coal Measures.

Anthracomya. Differs from *Carbonicola* chiefly in having the posterior part of the shell broad and expanded. Hinge-plate small, with a cardinal and one posterior lateral tooth. Carboniferous. Probably fresh water. Ex. *A. adamsi*.

Cardinia. Shell trigonal, oval, or oblong, very inequilateral, compressed, thick, marked by lines of growth. Interior not nacreous. Umbones small, sharp, close together. Ligament external. Cardinal teeth small or obsolete; in the right valve one anterior lateral tooth, in the left, one posterior lateral. Impression of anterior adductor very deep. Pallial line simple. Trias to Middle Jurassic (chiefly Lias). Ex. *C. listeri*, Lias.

Megalodon. Shell thick, equivalve, smooth or with concentric lines, convex, inequilateral, oval or rounded triangular. Umbones prominent, curved forward. Ligament external, long. Hinge-plate very large and thick; teeth thick; in the right valve two cardinals separated by a pit; in the left valve one cardinal under the umbo

and a small anterior cardinal; no laterals. Anterior adductor impression small, semilunar; posterior adductor long, shallow, on a ridge extending from the hinge to the posterior border. Devonian to Lias. Ex. *M. cucullatus*, Devonian. *Pachyrisma* (Trias and Jurassic) is allied to *Megalodon.*

5. Hinge heterodont; hinge-plate usually well-developed. Two nearly equal adductors. Ligament behind the umbones. Siphons usually well-developed. Shell without a pearly layer.

(*a*) Pallial line usually simple.

Cyprina. Shell orbicular or oval, convex, with concentric striæ and a thick periostracum. Umbones prominent, incurved. Ligament external, prominent. Lunule seldom present. Right valve with a small anterior cardinal below a triangular median cardinal, an oblique bifid posterior cardinal, and a posterior lateral. Left valve with a small anterior cardinal, a vertical median cardinal, and a long oblique posterior cardinal. Adductor impressions oval. Pallial line entire. Margins of valves smooth. Lias to present day. Ex. *C. islandica*, Coralline Crag to present day.

Isocardia. Similar to *Cyprina.* Umbones inflated, curved anteriorly or spirally inrolled. In each valve two nearly parallel cardinal teeth and one posterior lateral. Jurassic to present day. Ex. *I. cor*, Coralline Crag to present day.

Astarte. Shell thick, inequilateral, more or less trigonal or sub-orbicular, compressed, closed. Surface usually with concentric furrows or striæ. A thick periostracum is present. Umbones prominent. Lunule distinct. Escutcheon elongated. Ligament external. Two cardinal teeth in each valve, lateral teeth rudimentary. Adductor impressions strongly marked; above the anterior one is a pedal impression. Pallial line simple. Trias to present day. Ex. *A. omalii*, Coralline Crag.

Opis. Shell trigonal, cordiform, convex, with an oblique keel extending from the umbo to the posterior border. Umbones prominent, incurved or sub-spiral. Lunule large and very deep. Surface generally with concentric furrows. One cardinal tooth in the right valve, two in the left. Pallial line simple. Trias to Chalk. Ex. *O. lunulatus*, Inferior Oolite.

Crassatellites (=*Crassatella*). Shell solid, oblong or subtrigonal, attenuated behind. Surface smooth or concentrically furrowed. Margins of valves smooth or crenulated. Umbones small, close together. Lunule distinct. Ligament internal, placed in a pit under the umbo. Hinge with two (sometimes three) cardinal teeth, and some small laterals. Adductor impressions deep. Pallial line simple. Cretaceous to present day. Ex. *C. sulcatus*, Barton Beds.

Cyrena. Shell cordiform, oval, or trigonal, usually with concentric ridges; umbones often corroded. Hinge with three cardinal teeth; one anterior and one posterior lateral in the left valve, and two of each in the right valve. Ligament prominent, external. Pallial line usually entire. Lias to present day. Lives in fresh and brackish water. Ex. *C. ceylanica*, Recent.

Corbicula. Similar to *Cyrena*, but with the lateral teeth lamellar and transversely striated. Eocene to present day. Fresh water. Ex. *C. fluminalis*, Pliocene to present day.

Cardita. Shell oval or oblong, elongated, very inequilateral, with prominent radial ribs, usually scaly; often a little gaping and sinuous at its ventral margin. Umbones prominent, anterior. Lunule present. Ligament external. In the right valve two long, parallel cardinal teeth, and a small anterior lateral tooth. In the left valve one short anterior cardinal, and one long posterior cardinal, and a rudimentary posterior lateral tooth. Adductor impressions large. Pallial line simple. Trias to present day. Ex. *C. calyculata*, Recent.

Venericardia. Shell oval, triangular, or heart shaped, inequilateral, with radiating ribs. Umbones prominent. Ventral margin crenulated internally, not sinuous. Ligament external. Hinge-plate thick; in the right valve two oblique cardinal teeth and one small or rudimentary anterior lateral; in the left two diverging cardinal teeth. Adductor impressions unequal. Pallial line simple. Cretaceous to present day. Ex. *V. planicosta*, Bracklesham Beds.

Chama. Shell irregular, thick, inequivalve, fixed by the umbo of the larger valve (generally the left, sometimes the right). Umbones spiral or sub-spiral, directed anteriorly, that of the fixed valve longer than the other. Surface with concentric lamellæ or spines. The fixed valve larger and much deeper than the other. In each valve a strong

cardinal tooth, and sometimes in the inferior valve a narrow curved posterior tooth also. Ligament external, in a deep groove, prolonged towards the umbones. Adductor impressions large, the anterior commencing near the hinge-line. Pallial line simple. Upper Cretaceous to present day. Living in warm seas. Ex. *C. squamosa*, Barton Beds.

Diceras. Shell thick, inequivalve, fixed by umbo of larger valve. Umbones large, inrolled, directed forwards. Ligament external, in a curved groove at the posterior margin of the hinge. Hinge-plate very thick; right valve with a large, elongate, curved posterior cardinal tooth parallel to the ligament groove, and an anterior pit; left valve with a large ear-shaped cardinal tooth and a pit for the tooth of the right valve. Adductor impressions distinct, the posterior on a raised elongated plate. Pallial line simple. Upper Jurassic. Ex. *D. arietinum*. *Requienia* and *Toucasia* (Cretaceous) are related to *Diceras*.

Hippurites (figs. 109, 110). Shell very large and massive, conical or sub-cylindrical, not spiral, very inequivalve, fixed by the apex of the larger valve. The *large* (*lower*) *valve* elongate-conical, striated or smooth, and with three parallel furrows extending from the apex to the cardinal margin, due to folds of the shell-wall which give rise to three corresponding ridges in the interior. Hinge consists of a small cardinal tooth and of cardinal pits; anterior adductor impression large and divided into two separate parts; posterior adductor in a depression. *Small* (*upper*) *valve* flattened or slightly convex, operculiform, porous, the pores leading into canals; with a central umbo and two prominent teeth; the anterior tooth very large with two surfaces at its base for the attachment of the adductors; the posterior tooth smaller with a tooth-like process for the posterior adductor. The small valve is formed of two layers; the outer is thin and prismatic, the inner is porcellanous and traversed by numerous canals. The outer layer of the large valve is formed of small prisms arranged in parallel layers obliquely to the surface of the shell; the inner is porcellanous and formed of thin leaflets. Upper Cretaceous. Ex. *H. cornu-vaccinum*.

Radiolites. Shell large, thick, valves very unequal. The *large* (*lower*) *valve* conical or sub-cylindrical, generally straight, fixed by its apex (umbo); surface with vertical ribs, and thick, horizontal projecting layers which are more or less regularly folded; with a

ligamental fold extending from the apex to the margin, and two vertical undulations corresponding to the positions of the anal and branchial orifices; outer layer of shell very thick, formed of polygonal or prismatic cells; inner layer thin, porcellanous, often not preserved; an elongate median tooth; two adductor impressions widely separated. The *small* (*upper*) *valve* generally convex or conical, sometimes flat, with central umbo; two straight, elongate, grooved teeth; the two adductor muscles were attached to plates on either side of the teeth; shell structure similar to that of the larger valve, but with the external layer thinner. Upper Cretaceous. Ex. *R. angeiodes*. A Radiolitid (*Durania mortoni*) is found in the Chalk of England.

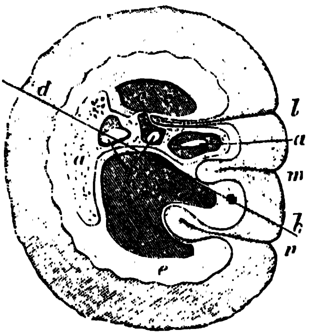


Fig. 109.

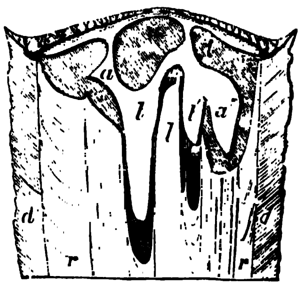


Fig. 110.

Fig. 109. Transverse section of the large valve of *Hippurites cornu-vaccinum*. *r*, umbonal cavity; *e*, internal layer of shell; *d*, external layer; *l*, *m*, *n*, folds; *t*, cardinal teeth; *a*, anterior adductor; *a'*, posterior adductor; *c*, cavity; *c'*, cardinal fossa. Cretaceous. (From Woodward.) $\times \frac{1}{3}$.

Fig. 110. Longitudinal section of the small valve and part of the large valve of *Hippurites cornu-vaccinum*. *u*, umbonal cavity of small valve; *d*, external layer of shell; *r*, internal layer; *i*, part of cavity between the valves; *a*, anterior adductor; *a'*, posterior adductor; *t*, *t'*, anterior and posterior cardinal teeth of small valve; *l*, cardinal tooth of large valve. (From Woodward.) $\times \frac{1}{2}$.

Unicardium. Shell oval or rounded, inflated; surface with concentric lines or ridges. Umbones prominent, curved inwards. In each valve a small cardinal tooth which is often obsolete, and a posterior ridge separated from the margin by a furrow in which is the external ligament. Adductor impressions elliptical. Trias to Cretaceous. Ex. *U. cardioides*, Lias.

Lucina (fig. 106 F). Shell orbicular or oval, slightly inequilateral, usually ornamented with concentric lines or ridges. Lunule usually distinct. An oblique furrow extends from the umbo to the posterior border. Hinge usually with two cardinal and one or two lateral teeth in each valve; the lateral, or the cardinal, may be absent. Ligament elongated, external, sometimes partly internal. Adductor impressions well marked, the anterior elongated and placed mainly within the pallial line, the posterior oval. Pallial line entire. Margins of valves smooth or finely crenulated. Trias to present day. Ex. *L. borealis*, Coralline Crag to present day.

Cardium. Shell convex, slightly inequilateral, cordate or oval, generally closed. Umbones prominent, incurved, turned slightly to the anterior end. Surface with radiating ribs, which are often spiny. Margins of valves crenulated. Right valve with one or two cardinal teeth, two anterior laterals, and one or two posterior laterals; left valve with two cardinals, one anterior lateral and one posterior lateral. Ligament external. Adductor impressions shallow. Pallial line entire. Trias to present day. Ex. *C. aculeatum*, Pleistocene and Recent; *C. edule*, Pliocene to present day.

Protocardia. Similar to *Cardium*, but with radiating ribs on the posterior part of the shell only, the remainder with concentric ribs. Jurassic to present day. Ex. *P. hillana*, Upper Greensand.

Thetironia (= *Thetis*). Shell thin, oval, rounded, very convex, slightly or moderately inequilateral. Umbones prominent, curved inward and slightly forward. No lunule. Ligament external. Two small conical or tubercular cardinal teeth under the umbo in each valve; no laterals. Adductor impressions near the anterior and posterior margins. Pallial line simple. Two internal ribs meet at an acute angle near the umbo and extend ventrally to the level of the adductors. Surface of shell nearly smooth, with concentric lines and radial rows of small pits which are more distinct on the posterior part than elsewhere. Cretaceous. Ex. *T. minor*, Lower Greensand.

(b) Pallial line usually with a sinus, but sometimes sinuous only.

Venus. Shell thick, oval, convex, ornamented with concentric lamellæ, sometimes with radial ribs; lunule distinct. Margins of valves finely crenulate. Hinge-plate wide; in each valve three cardinal

teeth, often bifid, no lateral teeth. Ligament external, prominent. Pallial sinus short, angular. Miocene to present day. Ex. *V. casina*, Pliocene to present day; *V. verrucosa*, Recent.

Meretrix (fig. 105). Shell thick, ovate, sub-trigonal, convex, smooth or with concentric ornament. Margins of valves smooth. Lunule present. Ligament external. Hinge-plate thick, with three cardinal teeth in each valve, two anterior laterals in the right, and one in the left valve. Pallial sinus angular or rounded. Cretaceous to present day. *M. meretrix*, Recent; Ex. *M. (Callista) planus*, Upper Greensand; *M. (Callista) chione*, Recent. *Meretrix* is here used in a wide sense, and includes *Callista*, *Cytherea*, *Tivela*, *Pitaria*, etc.

Dosinia (= *Artemis*). Shell orbicular, compressed, with concentric ridges or striæ. Lunule depressed. Escutcheon narrow. Ligament sunk. Three cardinal teeth in each valve, one anterior lateral in the left valve and two (rudimentary) in the right. Margins smooth. Pallial sinus very deep. Oligocene to present day. Ex. *D. exoleta*, Coralline Crag to present day.

Tellina. Shell oval, elongate, sometimes sub-orbicular, slightly inequivalve, compressed, rounded in front, attenuated behind, and furnished with an oblique fold from the umbo to the posterior border. Margins of valves smooth. Two cardinal teeth in each valve, and one anterior and one posterior lateral which are often indistinct in the left valve. Ligament external, prominent. Pallial sinus very deep. Jurassic to present day. Ex. *T. virgata*, Recent: *T. rostralis*, Eocene.

Psammobia (= *Gari*). Shell elongate, sub-equilateral, gaping at the ends, anterior side rounded, posterior side more or less truncate and angular. Surface smooth or with striæ. Ligament external, thick, joined to prominent ridges. Usually two cardinal teeth in each valve, some being bifid. Adductor impressions near the dorsal border. Pallial sinus very deep. Eocene (perhaps Cretaceous) to present day. Ex. *P. ferroensis*, Coralline Crag to present day.

Solen. Shell very long, sub-cylindrical, straight, smooth or finely striated, the dorsal and ventral margins parallel; gaping at both extremities. Margins of valves smooth. Umbones at the anterior end. Hinge terminal, with one cardinal tooth in each valve. Ligament long, external. Anterior adductor impression elongated, parallel to the dorsal margin. Pallial sinus short. Eocene (perhaps earlier) to present day. Ex. *S. obliquus*, Bracklesham Beds; *S. vagina*, Recent.

Mactra. Shell oval or trigonal, nearly equilateral, smooth or with concentric striæ. Internal ligament in a large triangular pit. External ligament in a groove. In front of the internal ligament-pit is a bifid cardinal tooth (in the form of an inverted V); anterior and posterior lateral teeth well-marked, compressed, double in the right valve, single in the left. Adductor impressions semicircular. Pallial sinus round or angular. Cretaceous to present day. Ex. ***M. ovalis***, Red Crag to present day

Mya (fig. 104). Shell oblong, gaping at both ends, particularly at the posterior; the left valve a little smaller than the right. In the left valve a large spoon-like process to which the internal ligament is fixed. Anterior adductor impression elongated. Pallial sinus large and rounded. Eocene to present day. Ex. ***M. truncata***, Pliocene to present day.

Corbula. Shell oval, inequivalve, closed, rounded in front, somewhat angular and contracted behind, with a ridge passing from the umbo to the posterior angle. Surface generally with concentric grooves. Umbones prominent. Right valve larger and more convex than the left, and with a strong cardinal tooth in front of the ligament-pit, and also a posterior cardinal tooth; left valve with a spoon-like process for the internal ligament, and one posterior cardinal tooth. Adductor impressions well marked. Pallial line slightly sinuous posteriorly. Trias to present day. Ex. *C. ficus*, Barton Beds; *C. sulcata*, Recent.

Panopea. Shell equivalve, inequilateral, oblong, thick, concentrically striated, gaping at each end, especially at the posterior. Ligament external, on a prominent ridge. One cardinal tooth in each valve. Pallial sinus very deep. Cretaceous to present day. Ex. *P. faujasi*, Coralline Crag to present day.

Saxicava. Shell small, more or less oblong, gaping; umbones anterior. Ligament external. Teeth absent in the adult, one or two cardinals present in the young. Pallial line not continuous, sinuous. *Saxicava* bores into rocks, etc. Jurassic to present day. Ex. ***S. rugosa***, Coralline Crag to present day.

Pholas. Shell elongate, cylindrical, gaping at both ends. Surface with spiny ridges, best marked in front. On the dorsal region are one or more accessory calcareous plates. No teeth; no ligament. In the interior, under the umbones, is a process for the insertion of

the muscle of the foot. Pallial sinus very deep. *Pholas* bores into rocks, etc. Eocene (perhaps Mesozoic) to present day. Ex. *P. cylindrica*, Red Crag; *P. dactylus*, Recent.

Teredo. Shell more or less globular, gaping at the ends, valves tri-lobed, with concentric striæ; without teeth; adductors unequal. In the interior, under the umbones, is a long narrow plate for the insertion of the pedal muscle. Posterior part covered by a long, calcareous tube, which is sub-cylindrical, straight or curved, and often with partitions. *Teredo* perforates wood. Jurassic to present day. Ex. *T. norvegica*, Coralline Crag to present day.

6. Hinge desmodont. Ligament usually behind the umbones. Two nearly equal adductors. Pallial line usually with a sinus, but sometimes sinuous only. Valves generally somewhat unequal.

Pleuromya. Shell transversely elongated, anterior side short, posterior long and generally compressed, sometimes gaping; surface with concentric folds. Hinge without teeth, but with a thin projecting lamina at the margin. Ligament partly external. Adductor impressions faintly marked; pallial sinus deep. Trias to Lower Cretaceous. Ex. *P. donacina*, Corallian and Kimeridgian.

Gresslya. Shell oval, elongate, very inequilateral, smooth or with concentric furrows; anterior side high and inflated, posterior side narrowing and somewhat compressed. Umbones anterior, close together; lunule sometimes well marked. Right valve a little higher and larger than the left. Adductor impressions shallow; pallial sinus deep. Behind the umbo of the right valve is a tooth-like projection and an internal plate—the latter appears as a furrow in casts of the shell. Jurassic. Ex. *G. gregaria*, *G. abducta*, Inferior Oolite.

Ceromya. Shell heart-shaped, inflated, inequilateral, finely granular, with concentric grooves. Left valve not quite so convex as the right. Anterior side short, posterior longer and compressed. Umbones prominent, anterior, curved forward. Hinge thickened, with a ridge behind the umbones; teeth absent. Pallial line sinuous. Jurassic. Ex. *C. concentrica*, Inferior Oolite to Cornbrash.

Pholadomya. Shell thin, translucent, oblong or oval, ventricose, equivalve, gaping posteriorly and sometimes anteriorly. Anterior side short and rounded. Surface with radiating ribs crossed by concentric folds or striæ. Umbones prominent. Ligament external. Hinge without teeth or with a small transverse tubercle. Adductor impressions very faint. Pallial sinus moderately deep. Lias to present day; abundant and widespread in the Mesozoic; two species living, one in the Antilles, one in Japan. Ex. *P. margaritacea*, London Clay.

Homomya. Similar to *Pholadomya.* Without radial ribs; surface smooth or ornamented with fine granules. Trias to Cretaceous. Ex. *H. gibbosa*, Inferior and Great Oolite.

Goniomya. Similar to the last two, but with V-shaped ribs pointing ventrally. Lias to Cretaceous. Ex. *G. literata*, Inferior Oolite to Corallian.

Thracia. Shell thin, oblong, compressed, attenuated and gaping posteriorly: surface smooth or concentrically striated. Umbones turned a little to the posterior side. Right valve larger than the left. External ligament short, prominent. Hinge thickened behind the umbo forming a stout process or ossicle in each valve to which the ligament is fixed. Adductor impressions small. Pallial sinus not deep. Trias to present day. Ex. *T. pubescens*, Coralline Crag to present day.

7. Shell thin. Hinge either without teeth or with only imperfectly developed teeth, and without hinge plate. Ligament external. Two nearly equal adductors. Pallial line simple. This group is a provisional one and includes primitive Palæozoic genera, the affinities of which have not yet been determined.

Grammysia. Shell elongate-ovate, very inequilateral, ornamented with concentric furrows, and one or more radial folds passing from the umbo to the postero-ventral border. Umbones placed anteriorly. Lunule very deep. Hinge-margin thick, without teeth. Anterior adductor very small, posterior large. Pallial line simple. Silurian and Devonian. Ex. *G. cingulata*, Silurian; *G. hamiltonensis*, Devonian.

Cardiola. Shell thin, convex, oval, generally inequilateral; umbones prominent, incurved. Surface with well-marked radiating and concentric grooves. Hinge-line straight, probably with very small teeth; ligamental area large, horizontally grooved. Muscular impressions unknown. Silurian and Devonian. Ex. *C. interrupta*, Lower Ludlow, etc.

Cardiomorpha. Shell thin, smooth or with concentric lines; sub-quadrate or rounded, inequilateral, very convex. Umbones prominent, curved forwards; no lunule. Hinge toothless. External ligament small. Adductor impressions shallow; pallial line simple. Principally Carboniferous. Ex. *C. oblonga*, Carboniferous Limestone.

Edmondia. Shell sub-quadrate or ovate, convex, inequilateral; surface with concentric lines or ridges. Umbones anterior; no lunule, no escutcheon. Hinge toothless, with a thick ridge posterior to the umbones and separated from the edge of the valve by a groove. Posterior to the hinge is an internal, elongated 'ossicle.' External ligament small. Pallial line simple. Devonian and Carboniferous. Ex. *E. unioniformis*, Carboniferous Limestone.

Sanguinolites. Shell elongate, very inequilateral, with rounded ends, the posterior part usually higher than the anterior part; surface with concentric ribs or lines. Umbones near the anterior end, with a ridge passing to the lower part of the posterior end; lunule and escutcheon distinct. Anterior adductor impression large, deep, limited posteriorly by a ridge; posterior adductor shallow, near the hinge. Pallial line entire. Hinge toothless. Carboniferous. Ex. *S. angustatus*, Carboniferous Limestone.

Distribution of the Lamellibranchia

All the Lamellibranchs are aquatic animals, and by far the larger number are marine. The marine forms range from the shore-line down to a depth of 2900 fathoms; they are most abundant in shallow water, and are scarce at depths greater than 500 fathoms, but the following, and a few other genera, have been found below 1500 fathoms:—

Nucula, Nuculana, Arca, Limopsis, Malletia, Verticordia, Cuspidaria (= *Neæra*).

Two genera, which may be Lamellibranchs, have been recorded from the Lower Cambrian of North America. In England the earliest forms appear in the Upper Cambrian (Tremadoc Beds). Lamellibranchs are not common in the Ordovician, but several genera are represented; they become fairly numerous in the Silurian, and afterwards gradually increase in importance, reaching their maximum at the present day. Many of the genera have a rather extended range in time.

In the Palæozoic formations the Taxodont and Dysodont groups, and primitive dimyarian forms with imperfectly developed hinges, are important. In the Carboniferous period *Carbonicola* and its allies and the Pectinidæ are well represented; only a very few forms with a pallial sinus (*e.g. Allorisma*) are found. Before the beginning of the Mesozoic period many of the Palæozoic genera became extinct, and in the Trias a number of new types appear. In the Mesozoic formations Dysodont, Isodont, Schizodont (Trigoniidæ), and Desmodont genera are abundant, and the Heterodont forms slowly increase. The Cretaceous period is particularly distinguished by the abundance of *Inoceramus*, and by the presence of *Hippurites, Radiolites* and other allied genera. In the Tertiary period the Heterodont group attains the greatest importance.

Fresh water lamellibranchs are generally rare in the Palæozoic and Mesozoic formations. Probably the earliest form is *Archanodon* (= *Amnigenia*) *jukesi* from the Old Red Sandstone. In the Coal Measures several species of *Carbonicola, Anthracomya*, and *Naiadites* occur. The living type *Unio* has been found in the Inferior Oolite of Yorkshire, and is fairly common in the Purbeckian and Wealden

of the south of England, where it is associated with *Cyrena*. Freshwater lamellibranchs also occur in the Woolwich Beds, the Oligocene deposits, and in the Pleistocene river-gravels.

The principal genera of Lamellibranchs found in the different systems are as follows:

Upper Cambrian. *Ctenodonta*, *Cyrtodonta*, *Glyptarca*.

Ordovician. *Ctenodonta*, *Cyrtodonta*, *Modiolopsis* and other allied genera.

Silurian. *Ctenodonta*, *Cardiola*, *Pterinea*, *Ambonychia*, *Modiolopsis*, *Grammysia*.

Devonian. *Nucula*, *Ctenodonta*, *Cardiola*, *Pterinea*, *Aviculopecten*, *Actinopteria*, *Megalodon*, *Conocardium*, *Grammysia*.

Carboniferous. *Nucula*, *Parallelodon*, *Posidonomya*, *Pinna*, *Conocardium*, *Leiopteria*, subgenera of *Pecten*, *Aviculopecten*, *Pterinopecten*, *Schizodus*, *Protoschizodus*, *Carbonicola* (= *Anthracosia*), *Anthracomya*, *Edmondia*, *Sanguinolites*, *Cardiomorpha*.

Permian. *Bakevellia*, *Schizodus*, *Pseudomonotis* (*Eumicrotis*).

Trias. *Nucula*, *Nuculana*, *Palæoneilo*, *Gervillia*, *Hoernesia*, *Pteria*, *Monotis*, *Cassianella*, *Halobia*, *Ostrea*, *Pecten* (subgenera), *Lima*, *Myophoria*, *Megalodon*, *Cardium*, *Palæocardita*.

Jurassic. *Nucula*, *Nuculana*, *Arca*, *Grammatodon*, *Myoconcha*, *Modiola*, *Hippopodium*, *Pteria*, *Pseudomonotis*, *Gervillia*, *Perna*, *Pinna*, *Ostrea*, *Gryphæa*, *Alectryonia*, *Pecten* (various subgenera of), *Lima*, *Cardinia*, *Trigonia*, *Diceras*, *Cardium*, *Unicardium*, *Astarte*, *Opis*, *Pachyrisma*, *Pleuromya*, *Ceromya*, *Gresslya*, *Pholadomya*, *Homomya*, *Goniomya*, *Thracia*.

Cretaceous. *Nucula*, *Arca*, *Cucullæa*, *Modiola*, *Myoconcha*, *Gervillia*, *Inoceramus*, *Perna*, *Pteria*, *Aucella*, *Aucellina*, *Ostrea*, *Exogyra*, *Alectryonia*, *Pecten* (the subgenera *Chlamys*, *Syncyclonema*, *Neithea*, etc.), *Lima*, *Spondylus*, *Plicatula*, *Unio*, *Trigonia*, *Hippurites*, *Radiolites*, *Sphærulites*, *Cardium*, *Protocardia*, *Thetironia*, *Cyprina*, *Cyrena*, *Callista*, *Panopea*, *Pholadomya*.

Eocene. *Nucula*, *Arca*, *Pectunculus*, *Pinna*, *Pecten* (*Chlamys*, etc.), *Ostrea*, *Chama*, *Cardium*, *Venericardia*, *Cardita*, *Astarte*, *Crassatellites*, *Cyprina*, *Lucina*, *Cyrena*, *Corbicula*, *Meretrix*, *Psammobia*, *Tellina*, *Corbula*, *Panopea*, *Pholadomya*.

Oligocene. *Mytilus*, *Dreissensia*, *Ostrea*, *Cyrena*, *Corbula*, *Erodona* (= *Potamomya*), *Lucina*, *Meretrix*, *Venus*, *Psammobia*.

Pliocene. *Nucula*, *Pectunculus*, *Mytilus*, *Pecten*, *Chlamys*, *Cardium*, *Cardita*, *Astarte*, *Cyprina*, *Isocardia*, *Lucina*, *Venus*, *Dosinia* (= *Artemis*), *Tellina*, *Mya*, *Pholas*, *Thracia*.

CLASS II. GASTEROPODA

Well-known examples of the Gasteropoda are the snail, the whelk, and the cowry. The bilateral symmetry, so characteristic of the lamellibranchs, is generally to a large extent obliterated, owing to the twisting of the visceral mass and the atrophy of some of the organs on one side of the body. There is a distinct head, which bears one or two pairs of tentacles, and usually also eyes. On the ventral surface of the body is the foot; this is usually large and sole-like and used for crawling, but in the Heteropods it is in the form of a flattened fin, and in the Pteropods it is wing-like. The mantle is never divided into two lobes. Respiration takes place in some cases through the skin, but generally by means of a lung-cavity or by gills; the latter are placed in a sac formed by the mantle; sometimes they are present on both sides of the body, but usually the original left gill has disappeared. In some forms the mantle, at the opening of the gill-sac, is produced into a tube, known as the *siphon*, by means of which water passes to the gills. The heart is on the dorsal surface, and consists of a ventricle and usually one, but in some cases two auricles. In many forms the gills are placed in front of the heart, but in others behind it. The mouth is at the anterior end of the body; the anus is occasionally posterior, but as a rule it is placed near the opening of the gill chamber. On the floor of the cavity of the mouth is a dental apparatus, known as the *odontophore*: this consists of a cartilaginous

and muscular ridge on which rests a chitinous ribbon (the *radula*); the radula bears numerous teeth placed in rows, and serves as a rasping organ. The arrangement of the teeth varies in different genera and is of considerable importance in classification, but since the radula has never been definitely recognised in fossil forms, it can only be used by the palæontologist in the case of genera which have existing representatives. In most gasteropods, except the carnivorous genera and the Heteropods, there are also one or two horny jaws in the upper part of the mouth which are used for biting. The nervous system consists of ganglia which are connected by nerve-cords. Typically there are three pairs of principal ganglia—the *cerebral* placed above the œsophagus, and the *pleural* and *pedal* placed below it; a visceral nerve-cord, which may bear ganglia, comes off from the pleural ganglia, and forms a loop ventral to the intestine. In some gasteropods (the Euthyneura) this loop is simple, but in others (the Streptoneura) one side is bent over so that the loop forms a figure of 8. Some gasteropods are unisexual, others hermaphrodite.

In the majority of the gasteropods a shell is secreted by the mantle; in a few forms, as for instance the slugs, it is internal, but usually it is external and covers the visceral mass. The shell, except in *Chiton* and its allies, consists of a single piece, and is hence said to be *univalve*. In the limpet (*Patella*) it has the form of a hollow cone; but in most cases it consists of a long tube, open at one end, and tapering to a point at the other. This tube is coiled into a spiral, generally screw-like, each coil being termed a *whorl*; in a few genera (*e.g. Vermetus, Siliquaria*) the whorls are separated, but as a rule they are in contact (fig. 111), the line between two contiguous whorls being known as the

suture (*su*). All the whorls, except the last, together form the *spire* (*S*) of the shell, the point of which is termed the *apex* (*a*). The last whorl is nearly always larger—frequently much larger—than the one preceding, and the part of it farthest from the apex is called the *base* of the shell. The spire varies in form in different genera and species; sometimes it is composed of a large number of whorls, sometimes of few, and it may be long, short, or depressed; occasionally all the whorls are in one plane. The angle of the spire (*spiral angle*) consequently varies; this is measured by lines drawn from the apex to the base of the shell on opposite sides of the exterior of the whorls. The coiling of the shell is usually *dextral*; so that when the apex of the shell is pointed away from the observer (as in fig. 111) the aperture will be on the right-hand side; in a few cases it is *sinistral*, when the aperture will be on the left.

Frequently the inner parts of the whorls coalesce, and form an axial pillar extending from the apex to the base of the shell (fig. 111) and known as the *columella*. In other cases the inner parts do not fuse, and in the place of the columella there is left a tube-like space, extending from the base of the shell a greater or less distance towards the apex; this space, which opens at the base of the shell, is called the *umbilicus*. When there is a columella the shell is said to be *imperforate*, when instead there is an umbilicus it is *perforate*. The opening of the umbilicus sometimes becomes partly or completely filled up with *callus* (see p. 248). The animal is attached to the columella by means of a muscle, the contraction of which enables it to withdraw completely into the shell; but, when not retracted, the coiled visceral mass only is covered by the shell.

Usually the cavity of the gasteropod shell is continuous

from the apex to the aperture, but in a few cases partitions are thrown across the earlier parts of the shell (fig. 111), forming chambers which remain empty. The form of the aperture varies considerably in different genera and is of great importance in classification; in shape, it may be circular, oval, elongate, oblong, etc. Its margin is termed the *peristome*: the outer part forms the *outer lip* (*L*), the

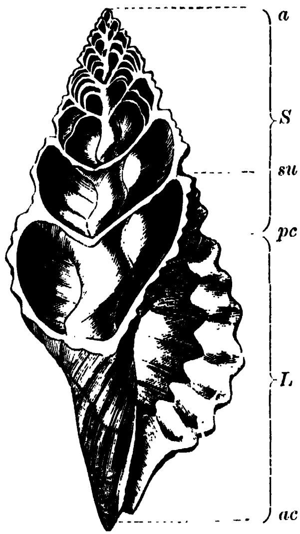


Fig. 111. Longitudinal section of *Tritonium corrugatum*. The upper part of the spire has been partitioned off many times successively. *a*, apex; *su*, suture; *S*, spire; *L*, outer lip of the aperture; *ac*, anterior canal; *pc*, posterior canal. (From Woodward.)

inner part (that next the columella) the *inner lip*. As the gasteropod crawls along, the shell is carried on the dorsal surface of its body with the apex directed backward and upward, and the aperture downward; consequently the part of the aperture farthest from the apex is *anterior*, the opposite (nearest the apex) is *posterior*. Sometimes,

as in *Natica*, there is no break in the peristome, and it is then said to be entire or *holostomatous*; in other cases the anterior border is notched or produced into a tube (*ac*) in which the incurrent siphon is placed, and these forms are said to be *siphonostomatous*; sometimes there is also at the posterior border another notch or a canal (*pc*), in which the excurrent or anal siphon is placed. The outer lip may be thin and sharp, or thickened. Sometimes it is curved outwards, and is then said to be *reflected*; or it is curved inwards —*inflected*. Its margin may be even, or crenulated, or produced into processes. In some genera a shelly deposit, termed *callus*, is secreted by the mantle on the inner lip and adjoining part of the last whorl.

Many genera have a calcareous or horny plate, known as the *operculum*, attached to the dorsal part of the posterior end of the foot; this is so arranged that when the animal withdraws into its shell the operculum more or less completely closes the aperture. It has been considered by some as a second valve, but more probably represents the byssus of the lamellibranch. The operculum is seldom preserved fossil; its form varies considerably in different genera, in some (*Turbo*) it is of very large size with the inner surface flattened and the outer convex; it may have a spiral structure, and is then sometimes formed of a large number of whorls (*multispiral*) as in *Trochus*, or of a few whorls (*paucispiral*) as in *Littorina*. When not spiral it may be *concentric*, if growth takes place equally all round; it is then marked with concentric lines, the nucleus being nearly central, as in *Viviparus*; or it may be *unguiculate* or *claw-shaped* when the nucleus is at the apex as in *Fusus*.

The form of the shell in the spiral gasteropods varies considerably, depending on the arrangement of the whorls in one plane or in a helicoid spiral, on the spiral angle, on

the number and shape of the whorls, on the size of the last whorl and whether it conceals the earlier whorls or not. The chief types are the following:—

1. *Discoidal;* all the whorls are nearly or quite in one plane, as in *Planorbis.*

2. *Conical* or *trochiform;* conical with a flat base, as in *Trochus.*

3. *Turbinate;* conical with a convex base, as in *Turbo.*

4. *Turreted* or *elongated;* as in *Turritella.*

5. *Fusiform;* tapering to each end, as in *Fusus.*

6. *Cylindrical;* as in *Pupa.*

7. *Globular;* spire short, last whorl large and rounded, as in *Natica.*

8. *Convolute;* when the last whorl covers all the others and the aperture is consequently as long as the shell, as in *Cypræa.*

9. *Auriform;* aperture very large and spire very short, as in *Haliotis.*

The surface of the shell is frequently ornamented with spines, knobs, ribs, or striæ; these are said to be *spiral* when they run parallel with the sutures, and *transverse* when they run across the whorls from suture to suture. In some genera (*e.g. Murex*) rows of spines, or lamellar processes, extend across all the whorls from the apex to the base of the shell, forming what are termed *varices.* The surface of the shell in recent gasteropods is generally coloured, often variegated; in fossil examples the colour has nearly always disappeared, but a few specimens, from various formations, even as early as the Carboniferous, have been found showing the colour more or less perfectly preserved. The shell consists of an outer chitinous layer, and of a calcareous layer, usually aragonite, which is thick and

porcellanous; in some cases there is also an inner nacreous or pearly layer.

The protoconch or embryonic shell is often found at the apex of the shell, and usually consists of several whorls differing in character from those of the rest of the shell. The gradual development of the ornamentation on the gasteropod shell may be traced on the whorls which follow the protoconch.

The Gasteropoda are divided into two sub-classes:—(1) Isopleura, (2) Anisopleura.

SUB-CLASS I. ISOPLEURA

The Isopleura include *Chiton* and its allies, and are often regarded as forming an independent class of the Mollusca. The body is bilaterally symmetrical and more or less elongated, with the anus at the posterior end. There are numerous (6 to 80) pairs of gills, which are placed in a groove between the foot and the mantle. A nerve-ring surrounds the œsophagus, and from it two nerves come off on each side and extend to the posterior end of the body; ganglia are poorly or not at all developed. The shell consists of eight plates placed in a longitudinal row on the dorsal surface of the body; each plate usually overlaps the one behind it, and a flexible band or girdle encircles the whole series of plates.

All the forms in this group are marine; they live chiefly in quite shallow water, but a few examples have been found at great depths. Although of great antiquity and represented by a large number of living species, the Isopleura are rarely found fossil. The earliest forms (*Priscochiton*) occur in the Ordovician; *Helminthochiton* is found in the Silurian; *Gryphochiton* and other genera in the Carboniferous; *Lepidopleurus*, *Chiton*, and others in the Tertiary.

SUB-CLASS II. ANISOPLEURA

The body is asymmetrical, owing to the twisting of the visceral mass. There are not more than two gills. The shell consists of one piece and is usually spiral. There are two orders, (1) Streptoneura, (2) Euthyneura.

ORDER I. STREPTONEURA

In the Streptoneura (or Prosobranchia) the visceral nerve-cord is twisted into a figure of 8. Usually one gill only is present, and it is generally placed in front of the heart. An operculum is found in most cases. The Streptoneura are divided into two sub-orders, (1) the Aspidobranchia, (2) the Pectinibranchia.

SUB-ORDER I. ASPIDOBRANCHIA

The axis of the gill is attached at its base only and bears two rows of plates (*bipectinate*). This group includes the more primitive gasteropods in which signs of the original symmetry are shown by the presence of two kidneys, two auricles and, in some cases, two gills.

Patella. Shell conical, oval or sub-circular; apex sub-central or excentric, nearer the anterior border, often curved forwards; surface with radiating ribs or striæ, rarely smooth. Margin simple or spinose. Muscular impression horse-shoe shaped, open in front. Jurassic (perhaps Palæozoic also) to present day. Ex. *P. vulgata*, Pliocene to present day.

Pleurotomaria. Shell trochiform, conical, turbinate, or nearly discoidal; interior nacreous. Umbilicus present or absent. Aperture sub-quadrate or oval, outer lip sharp, with a slit which, as the shell grows, becomes filled up, leaving a band on the whorls, towards which the lines of growth are directed obliquely backwards. Operculum horny. Silurian to present day; common and widespread in Jurassic, four species living in the seas of the West Indies and Japan at depths of from 70 to 200 fathoms. Ex. *P. anglica*, Lias; *P. ornata*, Inferior Oolite.

Murchisonia. Shell turreted, with many, more or less angular whorls, provided with a band as in *Pleurotomaria*. Aperture oblong, with a slit, and a very short anterior canal. Ordovician to Trias; mainly Devonian and Carboniferous. Ex. *M. verneuiliana*, Carboniferous Limestone.

Bellerophon (fig. 112). Shell globular, smooth or with growth-lines; umbilicus small or closed; whorls few, embracing, symmetrically coiled in one plane. Aperture sub-circular or oval, with a deep median slit, which is replaced by a band or keel dividing the shell into two similar parts; columellar edge often with callus. Ordovician to Permian; maximum in Carboniferous. Ex. *B. tenuifascia*, Carboniferous Limestone.

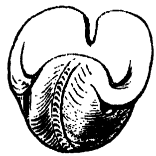


Fig. 112. *Bellerophon*, from the Carboniferous Limestone, showing the slit in the aperture. × ⅘.

Emarginula. Shell conical, surface generally ornamented with a trellis-work of longitudinal and transverse ribs; apex not perforated, curved posteriorly. Anterior border with a well marked slit, which becomes filled up during growth, leaving a raised band. Muscular impression horse-shoe shaped; no internal septum. Jurassic (perhaps Carboniferous) to present day. Ex. *E. fissura*, Coralline Crag to present day.

Fissurella. Shell similar to *Emarginula*, but more or less depressed; apex perforated and nearer the anterior than the posterior border; no marginal slit. Muscular impression as in *Patella*. *Fissurella* is divided into several sub-genera; many of the fossil species belong to the sub-genus *Fissuridea*. Jurassic to present day. Ex. *F. crassa*, Recent; *F. græca*, Coralline Crag to present day.

Euomphalus. Shell depressed, discoidal or conical, with a wide and large umbilicus; whorls convex with a ridge on the upper surface. Aperture polygonal; outer lip with a slit on its upper surface. Silurian to Trias; maximum in Carboniferous. Ex. *E. pentangulatus*, Carboniferous Limestone.

Omphalotrochus (=*Horiostoma* of some authors). Form similar to *Euomphalus*. Whorls ornamented with spiral keels and numerous transverse striæ or fine ribs. Aperture without a slit.

Ordovician to Carboniferous; common in Silurian. Ex. *O. discus*, Silurian.

Turbo. Shell solid, turbinate or conical, whorls convex, interior nacreous. Aperture large, circular, entire, slightly produced anteriorly; outer lip sharp. Columella curved, flattened. Imperforate, or with a small umbilicus. Operculum thick, calcareous, exterior convex, interior flat and spiral, nucleus central or subcentral. Jurassic to present day. Ex. *T. marmoratus*, Recent. There are numerous sub-genera.

Phasianella. Shell elongated, oval or oblong, smooth, polished, without an umbilicius, interior not nacreous. Aperture oval, entire, rounded anteriorly, angular posteriorly; outer lip thin, simple, sharp. Columella smooth, flattened. Operculum calcareous, with an excentric nucleus. Upper Cretaceous to present day. Ex. *P. australis*, Recent; *P. gosauica*, Upper Cretaceous.

Amberleya. Shell turbinate, elongate, without umbilicus. Whorls ornamented with several spiral keels which are usually spiny or nodular; between the keels are numerous transverse striæ or fine ribs. Base rounded. Aperture sub-oval; outer lip often crenulated. Trias to Cretaceous (chiefly Jurassic). Ex. *A. ornata*, Inferior Oolite.

Cirrus. Shell sinistral, conical or turbinate, or sometimes nearly discoidal, with a very large umbilicus. Spire acute. Whorls irregular, ornamented with strong transverse nodular ribs and finer spiral ribs; last whorl large. Aperture rounded, entire. Trias to Inferior Oolite. Ex. *C. nodosus*, Inferior Oolite.

Trochus. Shell conical, whorls numerous and flat or slightly convex, spire sharp, interior nacreous; base flat or nearly so, angular at the periphery. Aperture entire, rhomboidal; outer lip sharp, oblique. Columella twisted, with a prominent anterior tooth-like protuberance or a fold. Operculum horny, multispiral, nucleus central. Trias to present day. Ex. *T. niloticus*, Recent. There are numerous sub-genera.

Nerita. Shell thick, solid, ovoid or semi-globose, without an umbilicus; interior not nacreous. Spire very short. Surface smooth or with spiral ribs. Aperture semicircular, entire; outer lip thick, the interior generally denticulate; inner lip flattened, with callus, and a straight denticulate border. Operculum calcareous, nucleus

excentric. Cretaceous to present day. Ex. *N. ustulata*, Recent; *N. globosa*, London Clay and Bracklesham Beds.

Neritina. Form similar to *Nerita*. Shell relatively thin, usually smooth and with colour marking. Outer lip sharp, not thickened, with interior not denticulate; inner lip flattened, with sharp or finely denticulate border. Eocene (perhaps earlier) to present day. Lives in brackish or fresh water. Ex. *N. aperta*, Headon Beds; *N. zebra*, Recent.

SUB-ORDER 2. PECTINIBRANCHIA.

The gill is attached to the mantle throughout its length, and bears one row of plates only. There is no sign of bilateral symmetry in the circulatory, respiratory and excretory organs—only one kidney, one auricle, and one gill being present.

Macrochilina (=*Macrocheilus*), Shell elongate-oval, with sharp spire, and last whorl high. Surface smooth or with growth-line. No umbilicus. Aperture ovate, angular behind, sometimes with a shallow anterior canal; outer lip thin, inner lip with a weak anterior fold. Silurian to Trias. Ex. *M. arculata*, Devonian.

Loxonema. Shell turreted, spire very long; whorls convex, ornamented with sinuous growth-lines; sutures deep. No umbilicus. Aperture long, enlarging in front, with shallow canal; outer lip sharp, sinuous. Silurian to Trias (chiefly Carboniferous). Ex. *L. constrictum*, Carboniferous.

Pseudomelania. Shell elongate, with many nearly flat whorls, without umbilicus, spire long, surface smooth or with growth-lines. Aperture oval, entire, rounded in front, narrowed and angular behind; outer lip sharp. Columella smooth. Trias to Eocene; common in Jurassic. Ex. *P. heddingtonensis*, Corallian.

Scala (=*Scalaria*). Shell turreted, spire elongate; whorls numerous, very convex, sometimes separated, ornamented with strong transverse ribs or sometimes with lamellæ, frequently with spiral ribs also. Umbilicus more or less distinct. Aperture circular, entire, margin thickened. Operculum horny, paucispiral. Trias to present day. Ex. *S. scalaris*, Recent; *S. grœnlandica*, Red Crag to present day.

Solarium. Shell conical, depressed, angular at the periphery. Aperture entire, sub-quadrate; lip sharp. Umbilicus wide and deep, limited by a sharp edge which is generally crenulated. Operculum horny, spiral. Jurassic to present day. Ex. *S. perspectivum*, Recent; *S. canaliculatum*, Barton and Bracklesham Beds.

Purpuroidea. Shell thick, oval, spire rather short, last whorl inflated. Whorls step-like, flattened below the suture, with tubercles or spines at the angles. Aperture with a small notch anteriorly; outer lip thin. Inferior Oolite to Upper Cretaceous. Ex. *P. nodulata*, Great Oolite.

Littorina. Shell thick, without a nacreous layer, turbinate, with few whorls, without umbilicus. Aperture rounded, angular behind, outer lip sharp. Columella flattened. Operculum horny, paucispiral. Lias to present day. Ex. *L. littorea*, Red Crag to present day.

Capulus. Shell conical, with apex bent considerably backward and more or less spirally inrolled. Aperture rounded or irregular. Muscular impression horse-shoe shaped. Lower Palæozoic to present day. Ex. *C. hungaricus*, Coralline Crag to present day.

Platyceras. Allied to *Capulus*; apical part usually more extensively coiled, dextral. Surface smooth, or with concentric striæ, or radial folds or spines. Silurian to Carboniferous. Ex. *P. cornutum*, Silurian.

Calyptræa. Shell thin, conical, trochiform, spiral, apex central; interior with a spiral plate under the apex and attached at the periphery. Aperture nearly circular. Cretaceous to present day. Ex. *C. chinensis*, Coralline Crag to present day.

Natica. Shell oval, globular, generally smooth, spire short, last whorl very large. Aperture semi-lunar or oval, entire; outer lip sharp, inner lip thickened with callus, not crenulate. Umbilicus usually present, often filled with callus. Operculum of the same size as aperture, horny or calcareous, paucispiral, nucleus excentric. Trias to present day. Ex. *N. canrena*, Recent; *N. millepunctata*, Coralline Crag to present day. There are numerous sub-genera.

Xenophora (= *Phorus*). Shell conical, low, with flattened or concave base; periphery of last whorl sharp. Aperture large, oblique, lower part concave, outer lip sharp and oblique. Umbilicus generally

small. Whorls flattened, covered with agglutinated foreign bodies. Cretaceous to present day. Ex. *X. agglutinans*, Barton Beds.

Viviparus (=*Paludina*). Shell thin, turbinate, with a thick periostracum; whorls convex, smooth or with faint ribs. Umbilicus small or absent. Aperture entire, oval, slightly angular behind. Operculum horny with concentric striæ, and excentric nucleus. Inferior Oolite to present day. Lives in fresh water. Ex. *V. lentus*, Bembridge Beds.

Turritella. Shell without umbilicus, turreted, with many flat or slightly convex whorls, ornamented with spiral ribs and with striæ of growth; spire very long and acute. Aperture oval or sub-quadrate, entire, outer lip thin, slightly produced in front. Operculum horny. Trias to present day. Ex. *T. communis*, Pliocene to present day; *T. imbricataria*, Barton and Bracklesham Beds.

Melania. Shell with dark periostracum, elongate, turreted, with many whorls without umbilicus, apex sharp but usually corroded. Surface smooth, or ornamented with spiral striæ, or transverse ribs, or spines. Aperture entire, narrow behind, rounded in front; outer lip sharp, slightly sinuous behind. Columella smooth. Operculum horny, oval, sub-spiral. Wealden to present day. Lives in fresh water. Ex. *M. amarula*, Recent; *M. acuta*, Bembridge Beds.

Nerinea (fig. 113). Shell elongate, usually without an umbilicus, whorls numerous. Aperture sub-quadrangular, oval, or elongate, with a short anterior canal; outer lip thin, with a posterior slit near the suture, which becomes filled, leaving a continuous band. Columella and also the interior of the whorls furnished with folds which are continuous to the apex. Inferior Oolite to Upper Cretaceous. Ex. *N. cingenda*, Inferior Oolite.

Fig. 113. *Nerinea trachea*, partly sliced to show the form of the interior. Great Oolite. (From Woodward.) $\times \frac{2}{3}$.

Cerithium. Shell without an umbilicus, turreted, without periostracum. Whorls numerous, narrow, the last whorl always much shorter than the spire. Aperture oblong or semi-oval, with a short posterior canal and a well-marked recurved anterior canal; outer lip more or less thickened and often somewhat reflected; columellar edge concave. Operculum horny, oval, paucispiral, with submarginal nucleus. Jurassic to present day. Ex. *C. adansoni*, Recent; *C. mutabile*, Barton and Bracklesham Beds. There are several sub-genera. *Cerithium* in the restricted sense includes forms in which there is a strong ridge on the posterior part of the inner lip forming the inner boundary of the posterior canal, the outer lip is expanded in front, and the whorls are provided with varices. Ex. *C. nodulosum*, Recent.

Potamides. Form similar to *Cerithium*. Shell with a brown or blackish periostracum. Aperture rounded or sub-quadrangular; either with a fold in front or a very short and not recurved anterior canal; outer lip rather thin. Operculum circular, multispiral, with central nucleus. Lives in brackish water. Cretaceous to present day. Ex. *P. lapidus*, Eocene; *P. lamarcki*, Oligocene.

Aporrhais. Shell fusiform, without umbilicus, whorls numerous, spire elongate. Aperture produced in front into a straight or curved canal. Outer lip expanded, thick, with an anterior sinuosity, lobed or digitate, the posterior process being attached partly or entirely to a part of the spire forming a canal. Operculum small. Jurassic to present day. Ex. *A. pes-pelicani*, Coralline Crag to present day.

Dicroloma (= *Alaria*). Similar to *Aporrhais*, but without a process from the outer lip attached to the spire, and without anterior sinuosity. Jurassic and Cretaceous. Ex. *D. armata*, Great Oolite.

Strombus. Shell ovoid, ventricose, tuberculate or spiny, without umbilicus. Spire with several whorls. Last whorl very large. Aperture long, narrow, with a short anterior channel; canaliculate posteriorly; outer lip expanded, wing-like, thick, often lobed behind, with a sinus near the anterior margin. Operculum small, horny, claw-shaped, with serrated edge. Eocene to present day. Ex. *S. pugilis*, Recent.

Rostellaria. Shell fusiform, spire elongated, composed of many whorls, which are smooth or faintly ribbed. Aperture oblong, with a long straight or slightly curved anterior canal, and a posterior canal applied to the spire; outer lip expanded, with tooth-like processes, and an anterior notch. Operculum small, oval or claw-shaped, edge not serrated. Eocene to present day. Ex. *R. curta*, Recent; *R. lucida*, London Clay, etc.

Hippochrenes. Similar to *Rostellaria*, but outer lip wing-like and without processes. Upper Cretaceous and Eocene. Ex. *H. amplus*, Barton Beds.

Rimella. Similar to *Rostellaria*, but with cancellate ornamentation; outer lip but little expanded, and reflected outwards; canal reaching nearly to the apex of the spire. Eocene to present day. Ex. *R. rimosa*, Barton Beds.

* **Cypræa.** Shell ovoid or elongate, convex, convolute, surface covered with shining enamel. Spire almost or quite concealed by the last whorl. Aperture oblong and narrow, as long as the shell, with a short canal at each end; outer lip inflected and crenulated; inner lip crenulated. In the young form the outer lip is thin and the spire prominent. Eocene to present day. Ex. *C. mappa*, Recent; *C. oviformis*, London Clay. *Trivia* is similar but smaller and with transverse ribs. Eocene to present day. Ex. *T. europæa*, Recent.

Tritonium (fig. 111). Shell thick, oval or fusiform. Spire elongate, with varices which are continued over a few whorls only. Aperture with a posterior notch, and a slightly curved anterior canal; outer lip thick, crenulate internally; inner lip with callus and usually with folds. Eocene to present day. Ex. *T. variegatum*, Recent; *T. nodulosum*, Barton and Bracklesham Beds.

Buccinum. Shell oval or elongate, without an umbilicus. Spire of moderate length. Whorls ventricose, smooth or with longitudinal folds. Aperture oval, large; outer lip simple, thin; anterior canal short, truncated, a little reflected; columella a little sinuous. Operculum small, oval or circular. Eocene to present day. Ex. *B. undatum*, Coralline Crag to present day.

Nassa. Shell solid, ovate, elongate, without umbilicus, usually ornamented. Aperture oval, with a very short reflected anterior canal; inner lip with callus, reflected on to the last whorl, with a

ridge near the posterior end; outer lip thick, crenulate internally Columella truncated, provided with an oblique fold in front. Upper Cretaceous to present day. Ex. *N. mutabilis*, Pliocene and living.

Chrysodomus (= *Neptunea*). Shell solid, fusiform, spire more or less elongate, sometimes sinistral. Aperture oval; outer lip simple inner lip smooth; anterior canal short, slightly twisted. Operculum horny, unguiculate. Eocene to present day. Ex. *C. antiquus*, Red Crag to present day.

Purpura (= *Thais*). Shell tuberculate, striated or lamellar, without varices. Spire rather short, last whorl large; no umbilicus. Aperture oval, large, with either an anterior notch or a short oblique anterior canal, and a posterior notch or groove. Columella flattened with callus. Operculum lamellar, nucleus marginal. Miocene to present day. Ex. *P. persica*, Recent; *P. lapillus*, Red Crag to present day.

Murex. Shell thick, oval or elongate, spire prominent and sharp; whorls convex, each carrying three or more varices, which may be spiny, foliaceous, or tubercular. Aperture ovate; anterior canal more or less long, narrow and tubular, often nearly closed; no posterior canal; outer lip thick, inner lip smooth. Operculum oval, nucleus sub-apical. Eocene to present day. Ex. *M. brandaris*, Recent; *M. frondosus*, Barton Beds.

Typhis. Similar to *Murex*; small, with hollow spines; anterior canal short and completely closed. Eocene to present day. Ex. *T. pungens*, Barton Beds.

Fusus. Shell without umbilicus, narrow, fusiform, elongate; spire sharp, with many whorls. Aperture oval; outer lip simple, thin, interior often striated. A long, straight, narrow anterior canal, not closed. Columella smooth, without folds. Operculum oval. Cretaceous to present day. Ex. *F. colus*, Recent; *F. porrectus*, Barton Beds.

Clavilithes (= *Clavella*). Shell thick, usually large, fusiform, nearly smooth (except the earlier whorls, which have transverse and spiral ribs). Whorls often with a posterior carina near the suture. Aperture pyriform, channelled posteriorly, with a long straight anterior canal; outer lip thickened posteriorly. Last whorl contracting rapidly in front. Eocene to present day. Ex. *C. longævus*, Barton Beds; *C. parisiensis*, Middle Eocene.

Mitra. Shell fusiform, thick. Spire elevated, summit acute. Aperture narrow, elongate, notched in front. Columella with several oblique folds, of which the posterior are the stronger; outer lip not reflected, thickened, but not grooved internally. No operculum. Eocene to present day. Ex. *M. episcopalis*, Recent; *M.* (*Mitreola*) *labratula*, Bracklesham Beds.

Voluta. Shell thick, ovate, with short spire and turbinate protoconch. Last whorl very large; on the posterior part are nodules or spines which are continued anteriorly as transverse (or axial) ribs. Aperture elongate, with an angular channel at the posterior end; broad, and deeply notched at the anterior end; outer lip thick; inner lip with thin callus. Columella with several transverse, only slightly oblique folds, of which the four or five anterior are strong and nearly equal, and the posterior two or three are smaller. Eocene to present day. Ex. *V. musica*, Recent; *V. musicalis*, Eocene.

Volutospina. Shell fusiform, with rather short, conical spire; protoconch small, with sharp apex. Last whorl very large, tapering anteriorly. Whorls step-like, owing to the posterior part being flattened or concave; at the angle of the whorls is a row of spines (usually prominent) which are prolonged anteriorly as transverse (or axial) ribs; the latter are usually crossed by spiral ridges. Aperture elongate; at the posterior end one channel at the suture, another at the level of the row of spines; anteriorly the aperture is truncated and slightly notched. Outer lip usually thin; inner lip with thin callus. Columella with four or five very oblique folds, of which the anterior are stronger than the posterior. Upper Cretaceous to present day. Ex. *V. spinosa*, Eocene; *V. luctatrix*, Barton Beds.

Ancilla (= *Ancillaria*). Shell smooth, oval or oblong; last whorl large; sutures usually covered by callus. Aperture elongate, broadening anteriorly, with a small notch near the suture, and a deep sinuosity at the anterior end which is truncated; columella with callus posteriorly, twisted, and with folds anteriorly. Cretaceous to present day. Ex. *A. buccinoides*, Bracklesham, Barton, and Headon Beds; *A. cinnamonea*, Recent.

Pleurotoma (= *Turris*). Shell turreted, fusiform, spire long and sharp, last whorl long. Aperture oval, elongate; outer lip curved, with a deep slit at a short distance from the suture; inner lip smooth. Anterior canal long, straight, narrow. Columella without folds.

Operculum horny, ovate, acute, nucleus apical. Upper Cretaceous to present day. Ex. *P. babylonia*, Recent; *P. undata*, Bracklesham Beds. There are numerous sub-genera.

Conus. Shell conical, generally smooth, the last whorl enveloping the greater part of the preceding whorls. Spire short, flattened or conical, with many whorls. Aperture long, narrow, straight, with parallel or sub-parallel borders, ending anteriorly in a truncated canal; outer lip thin, simple, no folds or teeth, notched at the suture. Columella straight, smooth. Operculum horny, much smaller than the aperture. Upper Cretaceous to present day. Ex. *C. marmoreus*, Recent; *C. deperditus*, Bracklesham Beds. There are numerous sub-genera.

The Heteropoda are a group of the Streptoneura which have become modified for a pelagic mode of life. The foot is laterally compressed so as to form a vertical fin. A shell may be absent, but, when present, it is always thin and light. Only a very few forms have been found fossil.

ORDER II. EUTHYNEURA

The visceral nerve-cord forms (except in a few genera, *e.g. Actæon*) a simple, untwisted loop. One gill only is present. An operculum is generally absent. There are two sub-orders, (1) Opisthobranchia, (2) Pulmonata.

SUB-ORDER I. OPISTHOBRANCHIA

The gill is placed behind the heart; there is one auricle only, which is behind the ventricle. All the Opisthobranchia are marine; they are divided into two groups:—

(1) the *Nudibranchia*, in which there is no mantle, and no shell in the adult. No examples of this division have been found fossil;

(2) the *Tectibranchia*, which usually possess a mantle, a shell, and a true gill. The following genera are examples of the Tectibranchia.

Actæon. Shell oval, ornamented with spiral pitted striæ or grooves; spire prominent, conical, sharp. Aperture elongate, rounded in front; outer lip sharp; columella with one strong, slightly oblique fold at the anterior end. Cretaceous to present day. Ex. *A. tornatilis*, Coralline Crag to present day.

Avellana. Shell globular, ornamented with spiral striæ or grooves; spire very short. Aperture semi-lunar, curved, entire; outer lip much thickened, reflected externally, dentate internally. Inner lip thickened, with two or three prominent folds. Cretaceous. Ex. *A. incrassata*, Upper Greensand.

Bulla (= *Bullaria*). Shell solid, smooth, sub-globular or ovoid, convolute. Spire concave. Aperture as long as the last whorl, rounded at both ends, widest in front; outer lip sharp. Inner lip with callus. Cretaceous to present day. Ex. *B. ampulla*, Recent; *B. globulus*, London Clay and Bracklesham Beds.

The Pteropods are pelagic gasteropods in which the foot is modified to form two lateral wing-like fins, and the head is not well marked; a shell may or may not be present. Pteropods occur in large numbers near the surface in the open ocean, especially in warm regions; and their shells, which are thin and transparent, form a considerable part of the 'pteropod ooze'—one of the deep-sea deposits found in parts of the Atlantic Ocean.

By some writers the Pteropods have been regarded as a distinct Class of the Mollusca; by others as an Order of the Gasteropoda. Recent work on living forms, however, has shown that they agree very closely with the Opisthobranchia, and they are now generally regarded as specialised members of the Tectibranch group which have become adapted to a pelagic mode of life.

Living families of Pteropods, represented mainly by recent genera, occur in the Upper Cretaceous and Tertiary formations, but are not known from earlier deposits. In the Palæozoic formations, however, numerous fossils, which have been regarded by various authors as Pteropods, are

found. Thus in the Silurian and Devonian rocks large numbers of small conical smooth shells, which closely resemble the living *Styliola*, occur, and may be the remains of Pteropods.

Hyolithes (fig. 114), *Conularia*, *Tentaculites* and other allied genera are also found in the Palæozoic, beginning as far back as the Cambrian and Ordovician. Their shells, however, are larger and thicker than those of living Pteropods, and in *Conularia* they were, in some cases, attached by the apical end. Some writers have suggested that these Palæozoic genera are allied to primitive Cephalopods (such as *Volborthella*), since septa are sometimes present in the shell and possibly also a siphuncle. The recent discovery by Walcott of the presence of wing-like fins in a specimen of *Hyolithes* from the Middle Cambrian supports the view that that genus is really a Pteropod; if that is confirmed it follows that the Pteropods are the oldest group of the Opisthobranchs and cannot have been derived from the later Opisthobranchs which are not known before the Carboniferous period. The systematic position of *Conularia* and *Tentaculites* must still be regarded as doubtful.

Hyolithes (= *Theca*) (fig. 114). Shell calcareous, straight, rarely curved, pyramidal; its section triangular, elliptical, semi-elliptical or nearly circular; surface smooth or striated; posterior part sometimes crossed by septa. Aperture with an operculum. Cambrian to Permian. Ex. *H. elegans*, Ordovician.

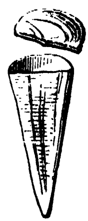


Fig. 114. *Hyolithes* from the Cambrian, showing the operculum. ×

Conularia. Shell thin, formed of chitin, more or less impregnated with lime; generally straight, pyramidal, with four sides; each angle of the pyramid with a straight groove;

each lateral face may have a median longitudinal groove. Apical part of shell sometimes with a few convex septa. Surface smooth, or ornamented with numerous transverse, parallel, angulated ridges, and sometimes with longitudinal ridges. Aperture partly closed by incurved triangular lobes. Ordovician to Lias. Ex. *C. quadrisulcata*, Carboniferous.

Tentaculites. Shell calcareous, thick, solid, in the form of a greatly elongated cone, straight or slightly curved, with circular section; apical part with septa, its end often with a vesicular enlargement. Surface provided with prominent, transverse, parallel rings, and with transverse and longitudinal striæ. Ordovician to Devonian. Ex. *T. anglicus*, Bala Beds.

Other genera, which appear to be allied to the preceding, are *Hyolithellus*, *Salterella*, and *Coleolus* from the Cambrian.

SUB-ORDER II. PULMONATA

The mantle-cavity is modified to form a lung. There is no gill. An operculum is nearly always absent in the adult. The Pulmonata are mainly land and fresh-water forms.

Limnæa. Shell spiral, thin, horny; last whorl very large, spire sharp. Aperture large, oval, rounded in front. Columella more or less twisted. Peristome sharp, entire. Purbeck Beds to present day. Lives in fresh water. Ex. *L. stagnalis*, Pliocene to present day; *L. longiscata*, Headon Beds, etc.

Planorbis. Shell discoidal, horny, whorls numerous. Aperture oblique; peristome simple, sharp. Jurassic to present day. Fresh water. Ex. *P. corneus*, Red Crag to present day; *P. euomphalus*, Headon Beds.

Helix. Shell variable—conical, discoidal, or globular; with or without an umbilicus; aperture oblique. Peristome simple or reflected. Eocene to present day. Lives on land. Ex. *H. nemoralis*, Pleistocene and living. There are numerous sub-genera.

Distribution of the Gasteropoda

Some of the Gasteropoda live on land, others in fresh water, but the majority are marine; they are found in the seas of all parts of the world but are especially abundant in warm regions and in comparatively shallow water. A few forms can exist both on land and in water, *e.g.* *Ampullaria*, which commonly lives in lakes and rivers, and is also found on land. Some marine genera, such as *Littorina*, *Cerithium*, and *Purpura*, are able to live in fresh as well as in salt water; on the other hand some fresh-water forms are at times found living in the sea, *e.g.* *Limnæa*, *Neritina*, *Bithynia*, and *Planorbis*; this is especially the case in places where the water is less salt than the main mass of the ocean, as for instance in the Baltic, where we find the genera just mentioned living side by side with *Littorina* and with the marine lamellibranchs *Cardium*, *Tellina*, and *Mya*. Two divisions of the Gasteropoda are entirely marine, viz. the Isopleura and Opisthobranchia; the Streptoneura (or Prosobranchia) are mainly marine. Nearly all the Pulmonata are found on land or in fresh water.

In this place a few words may be said with regard to the distribution of the marine Mollusca generally.

These may be divided into two groups belonging to the Plankton and the Benthos respectively.

The *Plankton* includes animals which swim or float either near the surface of the sea or at various distances below it; among the Mollusca the chief forms are the Pteropods, the Heteropods and a few other Gasteropods, as well as many Dibranchiate Cephalopods; the shells in these are either thin and light or altogether wanting. The geographical distribution of the species which live near

the surface is determined mainly by the temperature of the water.

The *Benthos* includes animals which are fixed to the sea floor or live crawling on it or swimming just above it. The distribution of the Mollusca in depth depends on the depth of the sea and the accompanying changes in temperature, pressure, light and other physical conditions. The Benthos may be divided into:

(1) The *Littoral zone*, which extends between high and low water marks and is consequently inhabited by animals which can live exposed to air for periods each day. In the European seas this zone is characterised by the abundance of the genera *Littorina, Trochus, Patella, Hydrobia, Haliotis, Fissurella, Solen, Mya, Donax, Cardium.*

(2) The *Continental shelf.* This includes the gradual slope from the low water-mark down to a depth of 100 or sometimes 200 fathoms, and extends to a distance of from 20 to 200 miles from land. It is on this part of the sea floor that most of the terrigenous deposits are laid down. The character of the molluscan fauna is influenced largely by the nature of the sediment on the sea-bottom, some genera (*e.g. Mya, Scrobicularia, Lutraria*) being found especially on muddy bottoms, others (*e.g. Natica, Turritella, Cypræa, Cardium*) on sandy, and yet others (*e.g. Buccinum, Littorina, Patella, Arca*) on rocky.

The upper part of the continental shelf from low water down to about 15 fathoms is known as the *Laminarian zone.* It is characterised by the great abundance of algæ (*Laminaria*, etc.) which afford food for numerous phytophagous molluscs; it is the region into which sunlight penetrates freely, the action of waves is felt, periodic changes of temperature occur, and the salinity is reduced owing to the drainage of fresh water from the land. In

the European seas some of the commonest genera are *Trochus, Nassa, Rissoa, Ostrea.* Nudibranchs are also very numerous.

Below the Laminarian zone the conditions become more uniform and less liable to sudden alteration. The changes in temperature are gradual, and seasonal rather than diurnal; the salinity is more constant, and light diminishes gradually with increasing depth and with it vegetation decreases. At a depth of about 100 fathoms (the lower limit of the continental shelf) the finer terrigenous materials are deposited forming what is known as the 'mud-line'—a rich feeding ground for animals.

The part below the Laminarian zone down to a depth of about 35 fathoms is known as the *zone of Nullipores or Corallines* on account of the numerous calcareous algæ (Corallinaceæ), and is characterised by the abundance of *Pleurotoma, Fusus, Chrysodomus, Buccinum, Natica, Eulima, Venus, Dosinia, Astarte, Nucula, Arca, Lima, Pecten.*

Below this is the *zone of Brachiopods and deep-sea Corals*; off Europe *Oculina* is the common coral; Brachiopods and Polyzoa are abundant. Some of the chief molluscs are *Turritella, Odostomia, Dentalium, Tellina, Cuspidaria* (= *Neæra*), *Yoldia.*

(3) The *Deep Sea and Abyssal Region* begins at the edge of the continental shelf with the relatively steep 'continental slope' extending down to about 500 fathoms, followed by the more gentle slope to the great deeps of the oceans. In this region light, except in the shallowest parts, is absent, the temperature is very low and nearly uniform at any one spot, currents are not felt, and the pressure of the water becomes very great. The only variation of importance is in the nature of the sediment which consists of fine ooze. The number of animals decreases

with the increase of depth. The shells of the molluscs are mostly thin, colourless, transparent and of small size. Scaphopods are numerous; other common forms are *Pleurotoma, Fusus, Actæon, Scaphander, Philine, Arca, Nucula, Limopsis, Nuculana, Lima, Pecten.*

Owing to the relative uniformity of the physical conditions the geographical distribution of the deep-sea species, although not unlimited, is greater than the range of the species which live on the continental shelf, especially on its shallower parts.

Of the Mollusca which live in shallow water or at moderate depths some few species have a very wide or almost cosmopolitan distribution, but the majority have a more limited range. In studying the geographical distribution of these Molluscs it is found that a number of areas or provinces can be recognised, each of which is characterised by the abundance of certain genera and species, and by the presence of some species which are either confined to that province or rarely found to extend beyond it; so that the general assemblage of molluscs found in each province possesses characteristic features. Two neighbouring provinces are not, as a rule, separated by a sharp boundary, and but few genera are confined to any one province. In the European and Northern Atlantic region the chief provinces[1] are: the *Arctic*, which includes the polar seas and extends as far south as the north coast of Iceland and the North Cape on the east of the Atlantic and to the shores of Newfoundland on the west; the *Boreal*, extending from the last down to near the southern end of

[1] For a map of the provinces see Woodward's *Manual of the Mollusca*, or Fischer's *Manual de Conchyliologie*, or *Encyc. Britannica*, ed. 11 (1911), p. 722.

Norway and including Iceland (except the north coast), the Färoe Islands and perhaps the Shetland Islands, and the American coast from the Gulf of St Lawrence to Cape Cod. The occurrence of the Boreal fauna on both sides of the Atlantic is accounted for by the former existence of a shallow coastal region across the North Atlantic along which this province was at that time continuous; the *Celtic*, including the coasts of Southern Sweden, the Baltic, Denmark, Northern France and the British Isles; and the *Lusitanian*, comprising the coasts of the Bay of Biscay, Portugal, the Mediterranean, and North-west Africa, including the Azores, the Canaries and Madeira groups. Altogether some nineteen provinces have been recognised, and these may be grouped into larger regions.

The chief barrier to the geographical extension of species is temperature, and consequently their range is influenced largely by the warm and cold currents in the surface waters of the sea. An example of this is seen in the North Atlantic where, owing to the cold Labrador current, the Arctic province extends much further south on the American coast than on the European; similarly, owing to the Gulf Stream drift the Boreal province is found further north on the European side than on the American. Another striking instance of the influence of currents is seen off South Africa; the warm water molluscs of the West coast are separated from those of the East coast by the cold water of the Antarctic drift which flows to the coast of Cape Colony, forming a barrier between the West African province and the Indo-Pacific province, thus causing the Cape province to have a special molluscan fauna.

The distribution of shallow-water molluscs is also interrupted by the presence of a wide and deep ocean.

Thus the fauna of the Indo-Pacific province which extends from East Africa along the coasts of the Indian Ocean to the Malay Archipelago, Northern Australia and the islands of the Pacific as far as 108° W., is prevented from reaching the American coast by the deep and broad Pacific Ocean.

Some species of molluscs which live in shallow water in cold regions are found to extend to temperate or tropical regions in deeper water where a similar temperature occurs. A few species are independent of both temperature and depth; thus *Venus mesodesma* was found on the shores of New Zealand at 55° F., and was dredged in 1000 fathoms at 37° F. off Tristan d'Acunha.

In the Palæozoic and Mesozoic formations gasteropods are generally less abundant than lamellibranchs, but they exceed them at the present day. The earliest forms occur in the Lower Cambrian Beds. Throughout the Palæozoic formations the holostomatous Streptoneura are the predominating forms; no gasteropods with a well-developed canal are known to occur until the Trias is reached, but siphonostomatous genera become fairly abundant in the Oolites, they increase still more in the Cretaceous, and in the Tertiary they are the principal forms. In the fossil state the other divisions of the Gasteropoda are not nearly so well represented as the Streptoneura. The Isopleura range from the Ordovician to the present day, but are rare as fossils. The Heteropoda are represented by a few forms only, the first occurring in the Miocene. The Opisthobranchia range from the Carboniferous to the present day; they are moderately well represented in the Jurassic and Cretaceous formations, and become more abundant in the Tertiary. Pteropods belonging to living types are found in the Upper Cretaceous and later formations, and earlier

forms which may belong to this group occur in the Palæozoic. Marine forms of Pulmonata appear first in the Devonian; non-marine forms are found in the Carboniferous, but are rare until the Purbeck and Wealden periods, and become abundant in the Tertiary deposits.

The most important genera of Gasteropoda found in the different systems are:—

Cambrian. *Scenella, Straparollina, Ophileta, Stenotheca.*

Ordovician. *Crytolites, Bellerophon, Holopæa, Raphistoma, Cyclonema, Maclurea, Subulites.*

Silurian. *Pleurotomaria, Bellerophon, Omphalotrochus, Holopæa, Cyclonema, Holopella, Platyceras.*

Devonian. *Pleurotomaria, Murchisonia, Bellerophon, Loxonema, Euomphalus, Macrochilina, Capulus.*

Carboniferous. *Metoptoma, Pleurotomaria, Murchisonia, Bellerophon, Loxonema, Euomphalus, Naticopsis, Macrochilina, Capulus.*

Permian. *Pleurotomaria, Murchisonia, Loxonema, Macrochilina.*

Trias. *Pleurotomaria, Trochus, Loxonema, Scala, Naticopsis, Natica, Turritella.*

Jurassic. *Pleurotomaria, Amberleya, Cirrus, Trochus, Natica, Pseudomelania, Bourguetia, Nerinea, Cerithium, Dicroloma* (= *Alaria*), *Malaptera, Purpurina, Purpuroidea.*

Cretaceous. *Pleurotomaria, Solarium, Turritella, Natica, Viviparus, Cerithium, Scala, Aporrhais, Dicroloma* (= *Alaria*), *Avellana.*

Eocene. *Xenophora, Calyptræa, Natica, Melanatria, Turritella, Cerithium, Rostellaria, Hippochrenes, Rimella, Aporrhais, Cypræa, Cassis, Cassidaria, Tritonium, Fusus, Clavilithes* (= *Clavella*), *Sycum* (= *Leiostoma*), *Pisania, Pyrula, Murex, Typhis, Voluta, Volutospina, Volutilithes, Oliva, Ancilla, Pleurotoma, Conus, Conorbis.*

Oligocene. *Nerita, Neritina, Natica, Viviparus, Melania, Melanopsis, Cerithium, Potamides, Murex, Fusus, Ancilla, Pleurotoma, Limnæa, Planorbis, Rissoa, Helix, Amphidromus.*

Pliocene. *Emarginula, Fissurella, Trochus, Scala, Turritella, Natica, Littorina, Capulus, Cerithium, Aporrhais, Trivia, Buccinum, Liomesus* (= *Buccinopsis*), *Tritonofusus, Chrysodomus, Nassa, Purpura, Trophon, Scaphella, Actæon.*

CLASS III. SCAPHOPODA

The Scaphopoda include only a few genera, which in some respects resemble the lamellibranchs, and in others the gasteropods. The body is elongated in an antero-posterior direction, and is bilaterally symmetrical. The mantle is nearly cylindrical, since its right and left margins are united ventrally; the mantle-cavity is open at both ends. The mantle secretes a nearly straight or slightly curved tubular shell which is also open at both ends, and gradually increases in width from the posterior to the anterior end; the concave side is dorsal. The foot is elongated and cylindrical; it can be protruded through the larger (anterior) aperture of the mantle and shell, and serves as a burrowing organ. The animal is attached to the posterior part of the shell by means of a muscle; an odontophore is present, but the head is rudimentary, and eyes, gills, and heart are absent. The sexes are separate. All the scaphopods are marine, and they usually live buried in sand or mud, with only the small posterior extremity projecting into the water; they range from the shore-line down to a depth of 2500 fathoms; only a few occur in the littoral zone, the majority being found in deeper water. The earliest forms are found in the Ordovician rocks.

Dentalium. Shell conical or sub-cylindrical, tapering posteriorly, slightly curved. Anterior aperture simple, not constricted; posterior aperture smaller, without a fissure. Surface ornamented with longitudinal striæ or ribs. Eocene to present day. Ex. *D. elephantinum*, Recent. Forms closely allied to *Dentalium* occur in many Palæozoic and Mesozoic formations.

CLASS IV. CEPHALOPODA

The Cephalopods are entirely marine and are more highly organised than other molluscs; well-known living forms are the cuttle-fishes, the squids, the paper-nautilus and the pearly nautilus, whilst amongst extinct types are belemnites, ammonites, and goniatites. Existing forms are always bilaterally symmetrical. The head is well marked and is separated from the body by a constriction; it is especially characterised by the presence of

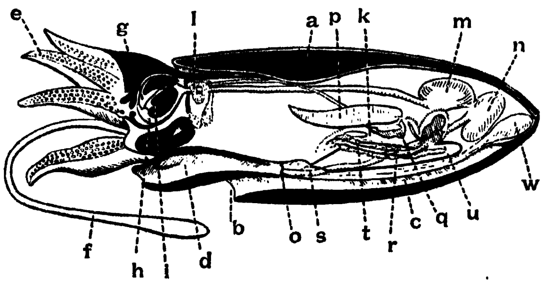


Fig. 115. Diagram of a vertical median antero-posterior section of *Sepia officinalis*. *a*, shell; *b*, mouth of mantle-cavity; *c*, mantle-cavity; *d*, funnel; *e*, arms; *f*, long arm; *g*, the upper beak or jaw; *h*, the lower beak or jaw; *i*, odontophore; *k*, the viscero-pericardial sac; *l*, the nerve-collar; *m*, the crop; *n*, the gizzard; *o*, the anus; *p*, left gill; *q*, ventricle of the heart; *r*, renal glandular mass; *s*, left nephridial aperture; *t*, viscero-pericardial aperture; *u*, branchial heart; *w*, ink-sac. (After Lankester.)

a circle of arm-like or lobe-like processes around the mouth (fig. 115, *e*, *f*); these processes are provided either with sucking-discs or with tentacles, and are used for seizing food, and in locomotion. Behind the head is a muscular tube termed the *funnel* (*d*), which opens in front to the exterior, and behind into the mantle-cavity (*c*); this may be either a perfect tube or may be formed by the apposition of two trough-like lobes. The arms or lobes around

the mouth are usually regarded as representing the fore-foot, and the funnel as the mid-foot, the hind-foot being absent. The name *Cephalopoda* is due to the view that the fore-foot has grown round the mouth and is divided up into arms or lobes. The part of the body near the mouth and funnel is usually regarded as ventral, and the opposite part as dorsal.

On the upper surface of the head there are two large eyes, which, except in *Nautilus*, are almost as highly developed as in vertebrate animals. The mantle is formed by a single fold of the skin, which passes quite round the body; on the anterior (upper) surface the fold is very shallow so that the mantle-cavity exists mainly on the posterior (under) surface. The feather-like gills (*p*) are placed in the mantle-cavity; in the Dibranchs (cuttle-fishes, etc.) there is one pair, in *Nautilus* there are two. A current of water flows in at the sides of the mantle-cavity, and can be forced out through the funnel by means of the contraction of the walls of the mantle-cavity. In the Dibranchiate Cephalopods there is a gland, known as the *ink-sac* (*w*), which secretes a black fluid (sepia); the duct from this gland opens with the anus (*o*) into the mantle-cavity; the ink is ejected at times and passes out through the funnel, rendering the water cloudy, and by this means facilitating the escape of the animal from its enemies. Just within the mouth there are two jaws (*g*, *h*) which have the form of a parrot's beak, and are either horny or calcareous. An odontophore (*i*) is also present, but the arrangement of the teeth is less variable than in the gasteropods, and is of little value for systematic purposes.

The heart consists of a median ventricle (*q*), and of lateral auricles, which are either two or four in number,

according as there are two or four gills. The nervous system is remarkable in that the ganglia are placed close together, forming a central mass (*l*); one part is placed above the œsophagus, and is connected by cords with the other part beneath it. This central nervous system is covered by a cartilaginous ring and gives off nerves to the arms, viscera, etc. The sexes of the Cephalopods are always separate, and show external differences. In some genera there is no shell; but when present it may be external (fig. 116) or internal (fig. 115, *a*); in the latter case it is usually placed in a sac formed by folds of the mantle on the antero-dorsal side. The Cephalopoda are divided into two Orders:—(1) Tetrabranchia, (2) Dibranchia.

ORDER I. TETRABRANCHIA

The Tetrabranchia have four gills, and an external chambered shell. There are two Sub-Orders, (1) Nautiloidea, (2) Ammonoidea.

SUB-ORDER I. NAUTILOIDEA

In Palæozoic times the Nautiloid Cephalopods were very abundant, but at the present day the only representative of the group is *Nautilus* (fig. 116). This possesses two pairs of gills, and two pairs of auricles; no ink-sac is present; and the funnel is not a complete tube, but is formed of two parts. Around the mouth are numerous lobe-like processes which are given off from the margin of the head; these represent the arms but do not bear suckers, as is the case in the Dibranchs, but tentacles which can be retracted within sheaths. The *hood* (fig. 116, 2) is a structure formed by the enlargement of the outer lobe of the foot and serves to close the aperture when the

animal withdraws into the shell. The jaws are calcified and are not uncommonly found fossil. The eyes are of simple structure, consisting of a hollow chamber with a pin-hole opening without lens or cornea.

A shell is present in all Nautiloids and is always external; it consists of a tube, which tapers to a point at one end, and may be straight, arched, or spiral. In the

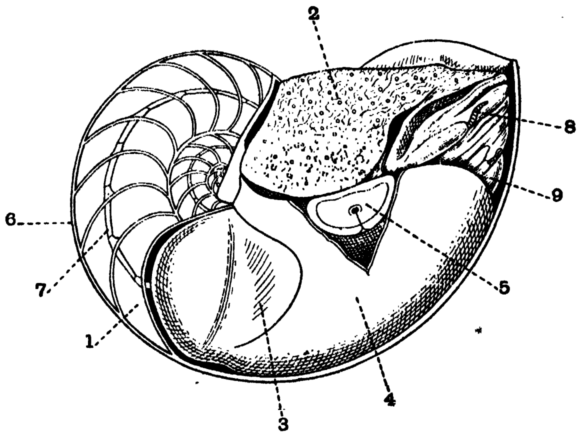


Fig. 116. *Nautilus pompilius.* Half the shell has been removed. 1, last completed chamber; 2, hood part of foot; 3, shell muscle; 4, mantle, cut away to expose the eye (5); 6, outer wall of shell; 7, siphuncle; 8, tentacle-bearing lobes of foot; 9, funnel. (After Graham Kerr.) × ½.

spiral forms the whorls may be separate, or partly free, or in contact throughout; commonly they are all in one plane, but in some cases they form a helicoid spiral. The interior of the shell, unlike that in most gasteropods, is divided into a number of chambers by means of transverse partitions termed septa (fig. 117, *b*); generally the chambers increase in size towards the aperture of the shell. The body of the animal occupies the last or *body*-

chamber (*a*), to the walls of which it is attached by muscles (fig. 116, 3); in *Nautilus* there are two oval muscular impressions, one on each side, near the last septum and the inner side of the whorl; these impressions are marked by faint concentric lines. The muscles are connected both above and below by a band of fibres called the *annulus*, which likewise leaves a mark on the shell. In *Nautilus* the funnel is placed at the external margin of the aperture, so that this part of the last chamber is regarded as ventral.

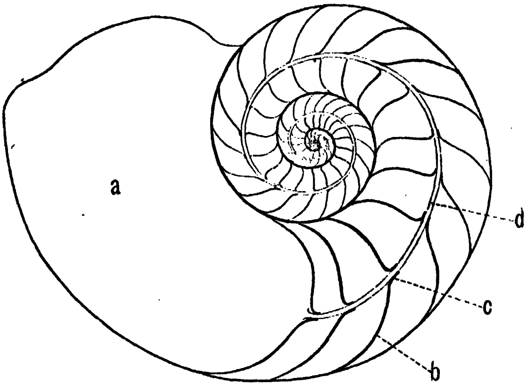


Fig. 117. Section of the shell of *Nautilus pompilius*, Recent. *a*, body-chamber; *b*, septum; *c*, septal neck; *d*, siphuncle. $\times \frac{1}{3}$.

All the chambers, except the body-chamber, are filled with air, giving buoyancy to the shell. The shell grows by the addition of material at the margin of the aperture; after a certain period the body of the animal moves forward and a new septum is secreted behind it, thus cutting off a new air chamber. This movement occurs after a period of growth, and is not related, as some have supposed, to periods of reproduction, since it is only after the shell is completed that reproduction begins. In

Nautilus the last air chamber of the completed shell is usually somewhat smaller than the preceding one (fig. 117). All the air chambers are traversed by a slender cord-like prolongation of the dorsal end of the body, containing arteries, and known as the *siphuncle* (fig. 116, 7; 117 *d*). The position of the siphuncle varies in different genera; in *Nautilus* it pierces the septa at or near their centres; in others it may be near either the external or the internal margin of the whorl. In the modern *Nautilus* the siphuncle has only a thin calcareous covering; but in many fossil Nautiloids it is completely invested by a calcareous tube. In Palæozoic genera the interior of the calcareous siphuncle is frequently partly filled up with calcareous deposits. The septa are often prolonged in the form of funnels around the siphuncle, so as to more or less completely insheath it; they may be short or may reach from one septum to the next or even further; these funnels are termed *septal necks* (fig. 117, *c*; 118 *d*); in nearly all the Nautiloidea they are directed backwards (retrosiphonate).

The aperture of the shell has, in some cases, a simple margin, being either straight or slightly curved; in others, processes are given off from the external margin or from the sides; in *Nautilus* there is a sinus at the external (ventral) margin where the funnel occurs, and the lines of growth on the shell are correspondingly curved. In some fossil Nautiloids (*Phragmoceras*) the sinus is at the inner margin of the aperture, which was therefore presumably ventral. In a few forms (*e.g. Gomphoceras*, fig. 120) the aperture, owing to the inward growth of the margin of the body-chamber, is constricted.

The line where the edge of the septum unites with the outer or tubular part of the shell is known as the *suture*;

obviously this will only be seen when the shell is removed; but fossil forms frequently occur as casts and in these the sutures are clearly shown. One of the chief characters of the shell in the Nautiloidea is the simple form of the sutures; usually they are either straight or only slightly undulating.

The shell which covered the embryo in the Cephalopoda is known as the *protoconch*[1]; in the Nautiloidea this probably consisted of non-calcified material, and is not definitely known to be preserved in fossil specimens; but some authors have found calcareous protoconchs in straight conical shells which they believe to belong to the genus *Orthoceras*. If the shell of a *Nautilus* be sliced in two, there will be seen at the centre a space (fig. 118, *a*) which was probably occupied by the protoconch. At the apex of the first chamber is an opening which is usually slit-like and surrounded by either a rim or a depression; this opening probably served to connect the protoconch with the first chamber. The siphuncle (*c*) commences in the first chamber as a closed tube.

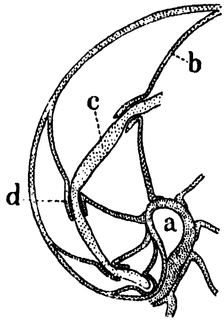


Fig. 118. Median section of the central part of the shell of *Nautilus*. *a*, central space; *b*, septum; *c*, siphuncle; *d*, septal neck. Enlarged.

Orthoceras. Shell straight or occasionally slightly curved, elongate-conical; transverse section usually circular. Septa concave; body-chamber large; aperture not contracted or produced into lobes. Siphuncle cylindrical, without internal calcareous deposits; usually

[1] This corresponds to the protegulum of the Brachiopods and to the prodissoconch of the Lamellibranchs.

central, but sometimes sub-central or ex-central. Ornamentation variable. *Orthoceras*, as defined above, includes numerous species which have grouped into more restricted genera based mainly on the character of the ornamentation. Tremadoc Beds to Trias. Ex. *O. intermedium*, *O. annulatum*, Silurian; *O. goldfussianum*, Carboniferous Limestone.

Actinoceras (fig. 119). External form similar to the preceding; often very large; section usually elliptical. The siphuncle is large, and inflated between the septa so that each segment is spheroidal, and contains in the interior a large amount of calcareous deposit. In the centre of the siphuncle is a small tube known as the *endosiphon* (*d*), from which radiating tubes (*c*) are given off between the septa and pass to the siphuncle. Ordovician to Carboniferous Limestone; in England chiefly Carboniferous. Ex. *A. giganteum*, Carboniferous Limestone.

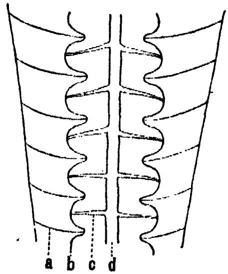


Fig. 119. Diagrammatic section of a portion of the shell of *Actinoceras*. *a*, septum; *b*, siphuncle; *c*, canals from endosiphon; *d*, endosiphon.

Gomphoceras (fig. 120). Shell ovoid, short, straight or slightly curved; section nearly circular; body-chamber very large, aperture contracted, T-shaped. Septa close together. Siphuncle sub-cylindrical or beaded, sub-central, placed nearer the more convex side of the shell. Surface smooth or with transverse ribs or striæ. *Gomphoceras* has been divided into several 'genera' based mainly on the form of the aperture. Ordovician to Devonian. Ex. *G. ellipticum*, Lower Ludlow.

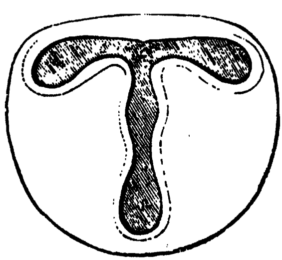


Fig. 120. Aperture of *Gomphoceras* (*Mandaloceras*) *bohemicum* from the Silurian. (From Woodward.) Natural size.

Phragmoceras. Similar to the last, but curved and rapidly increasing in diameter, laterally compressed, section oval or elliptical; siphuncle near the inner (concave) margin. Silurian. Ex. *P. broderipi.*

Ascoceras. Shell a little curved; the earlier part (which is rarely found) is similar to *Orthoceras*, but with the septa more widely separated. The later formed part is sac-like and a little more convex on the outer than on the inner side; the body-chamber occupies most of the outer side; the septa join together and then bend round and divide again before reaching the inner side of the shell; the siphuncle of this part is very short. Ordovician, but chiefly Silurian. Ex. *A. bohemicum*, Silurian.

Cyrtoceras. Externally similar to *Orthoceras* but always curved: never forming a complete volution; section usually elliptical or oval. Siphuncle small, cylindrical or bead-like, usually sub-marginal and usually near the convex side of the shell. The numerous species of *Cyrtoceras* have been divided into groups regarded as genera. Cambrian to Carboniferous. Ex. *C. lineatum*, Devonian.

Poterioceras. Shell smooth, fusiform, slightly curved, inflated in the middle, contracted at both ends, but especially at the apical end. Section elliptical in the adult. Siphuncle sub-central or marginal, inflated between the septa. Last chamber large, aperture simple, contracted. Ordovician to Carboniferous. Ex. *P. fusiforme*, Carboniferous Limestone.

Nautilus (figs. 116, 117). Shell more or less globose, spiral, whorls few, coiled in one plane, and more or less completely embracing. Umbilicus usually small or absent. Last chamber much larger than the preceding one, aperture simple, with an external sinus. Septa concave, sutures more or less undulating. Siphuncle central or subcentral, septal necks short and directed backwards. Surface of shell smooth or ornamented with striæ or ribs. Trias to present day. Ex. *N. pompilius*, Recent; *N. pseudolineatus*, Inferior Oolite.

Discites (= *Discitoceras*). Shell spiral, compressed, discoidal; whorls quadrangular in section, increasing in size gradually, sometimes a little embracing, with the external margin flat or grooved, and the sides flattened. The last part of the shell is separated from the preceding whorl for a short distance. The earlier whorls have longitudinal ribs. Carboniferous Limestone. Ex. *D. leveilleanus*. Other Carboniferous genera with plane spiral shells are *Cœlonautilus*, *Temnocheilus*, *Vestinautilus*.

Aturia. Shell discoidal, whorls compressed, completely embracing, with rounded external margin; suture-line zigzag, with a

deep angular lobe on each side. Siphuncle near the internal margin; septal necks large and very long, completely covering the siphuncle. Eocene and Miocene. Ex. *A. zic-zac*, Eocene.

SUB-ORDER II. AMMONOIDEA

The Ammonoids are quite extinct and include the ammonites, goniatites, etc. The shell is generally coiled into a plane spiral, and as a rule the sutures show complicated patterns (fig. 121). The siphuncle is at the

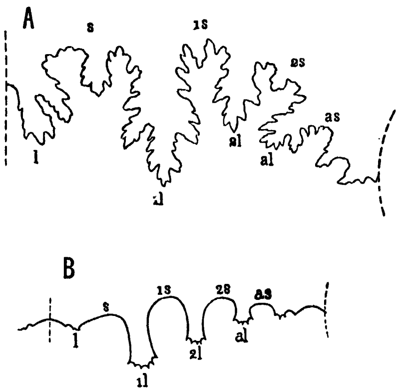


Fig. 121. A. Suture of an Ammonite (*Parkinsonia dorsetensis*) from the Inferior Oolite. B. Suture of *Ceratites nodosus*, from the Muschelkalk. *l*, one half of the external lobe; 1*l*, 2*l*, superior and inferior lateral lobes; *al*, auxiliary lobes; *s*, external saddle; 1*s*, 2*s*, superior and inferior lateral saddles; *as*, auxiliary saddles. In each case the straight line on the left represents the position of the siphuncle at the external margin, and the curved one on the right the line of contact with the next whorl.

margin of the shell—generally at the outer, but occasionally at the inner margin; it is usually more slender than in the Nautiloids and does not contain internal calcareous deposits. The septal necks in the ammonites are directed forwards (prosiphonate), except in some of the earliest chambers; in *Clymenia* and some goniatites, on the other hand, they point backwards as in the Nautiloids

(retrosiphonate); but in the more advanced types of goniatites they are transitional, a small collar-like part projects in front of the septum, but the main part of the septal neck extends backwards.

The form of the sutures varies considerably in different genera and is of great importance for systematic purposes. The central part of each septum is flattened or slightly undulose, but the edges become folded or even frilled, often giving rise to very complex sutures; by this means greater support is afforded to the outer tubular part of the shell than is the case in the Nautiloids where the sutures are simple. The portions of the suture which are convex towards the mouth of the shell are termed *saddles* (fig. 121, *s*), while the intervening concave portions are known as the *lobes* (*l*). In many forms the lobes and saddles exhibit secondary foldings, which may be slight, producing merely a denticulate pattern, or may be deep and provided with other smaller foldings, giving a foliaceous appearance to the suture. The lobes and saddles are nearly always similar on the two sides of the shell: commonly there is first the *external lobe* (fig. 121, *l*) at the external margin, then the *superior* and *inferior lateral lobes* on the sides of the whorl (1 *l*, 2 *l*), and near the inner margin other lobes known as *auxiliary lobes* (*al*) may occur; on the internal margin (opposite to the external lobe) is the *internal lobe.* The saddles are arranged in a similar manner; there are the *external saddle* (*s*), the *lateral saddles* (1 *s*, 2 *s*), and *auxiliary saddles* (*as*). The external lobe is often divided by a median saddle (as in fig. 121). The form of the successive sutures remains almost constant on the adult part of the shell, but on the younger parts the sutures are less complex. The suture of the first septum may be straight or only slightly curved, as in the Nauti-

loids; or it may show a broad external saddle; or a narrow external saddle with a lateral lobe on each side. In the second and later septa the sutures become successively more folded, until the adult form is attained. In the early Ammonoids the sutures are comparatively simple; the minor divisions of the lobes and saddles begin to appear in some Carboniferous genera; they increase in importance in the Permian and attain a great development in the Trias where the ammonites commonly possess very complex sutures.

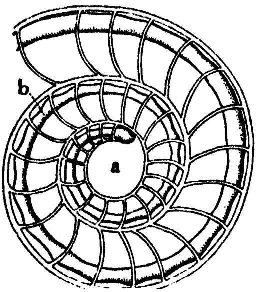


Fig. 122.

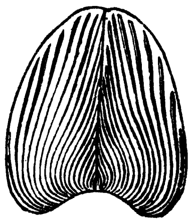


Fig. 123.

Fig. 122. Section, just above the median plane, of the early part of an ammonite—*Amblycoceras planicosta*, Lias. *a*, protoconch; *b*, siphuncle. (After Branco.) ×21.

Fig. 123. Aptychus of an ammonite, from the Oxford Clay. (From Woodward.)

The protoconch of the Ammonoids, unlike that of the Nautiloids (p. 279), is formed of calcareous material, and is often preserved; it is spherical or ovoid in shape and spirally coiled (fig. 122 *a*). The first septum closes the aperture of the protoconch. The siphuncle (*b*) commences with a bulbous enlargement which projects into the protoconch; in the first few chambers it is nearly central and relatively large, but afterwards it gets gradually nearer the external margin of the whorl and becomes relatively smaller.

In the body-chamber of some ammonites and goniatites, and in *Baculites* and *Scaphites*, a pair of calcareous plates, known as the *aptychus* (fig. 123), are occasionally found; in shape they are triangular or nearly semi-circular; the margins where the two plates are in contact are straight, the others curved. Since in one ammonite an aptychus was found closing the aperture of the shell, it is probable that it served as an operculum (p. 248) and was attached to a part of the body representing the hood of Nautilus (fig. 116, 2). A similar structure, but consisting of chitin, and with the two plates united, is found in the body-chamber of some ammonites.

In a few Ammonoids the shell is either a straight cone (*e.g. Bactrites*) or coiled into a helicoid spiral (*e.g. Turrilites*), but in the great majority of the genera all the whorls are in a plane spiral, and in such the form of the shell depends mainly on whether the later whorls grow round the earlier, or are simply in contact with them or slightly separated; in some genera the last whorl partly (fig. 134) or completely (fig. 127) conceals all the previous ones, but in others (fig. 129) the whole of the whorls are visible, and then the umbilicus—which is present on both sides of the shell—is very large. When the diameter of the whorl from side to side (*i.e.* the *thickness*) is greater than the diameter from the internal to the external margin (*i.e.* the *height*) then the umbilicus becomes deep, and if in such cases the later whorls embrace the earlier, then the umbilicus will be both deep and narrow.

The surface of the shell may be smooth or ornamented with striæ, ribs, tubercles, or spines; as a rule the ornamentation is much more developed in Mesozoic than in Palæozoic genera. In some ammonites (fig. 132) the external margin of the shell is provided with a ridge or *keel*, and in these forms the ribs of the two sides are not con-

tinuous. The keel may be smooth or toothed. In some genera there is either a groove or a flattened margin in place of the keel. The aperture of the shell in the ammonites is frequently produced into lobes at the sides, or into a pointed projection at the external margin (figs. 132, 133). In some of the goniatites there is a sinus at the external margin of the aperture indicating the position of the funnel, but this disappears in the more advanced types.

The character of the ornamentation, the shape of the whorls, and the form of the sutures, change at different periods in the life of the individual; these changes, which occurred during growth from the protoconch up to the adult, can be traced out by examining the early whorls of the shell. From a study of this development of the individual (ontogeny) attempts have been made to trace out the phylogeny of various types of Ammonoids. As in the case of the Brachiopoda (p. 178) it has been found that some forms, which in the adult state appear to be nearly identical, differ in their development, indicating that they have descended from different ancestors. Similarly, the development of the sutures and other features of the shell show that the ammonites have descended from more than one group of goniatites.

The most primitive of the Ammonoids, and apparently the ancestral form of the goniatites, is *Bactrites*, found in the Devonian and Lower Carboniferous; it possesses a straight or slightly curved tapering shell with the siphuncle at the margin, and the sutures are simple except for the presence of a funnel-shaped lobe at the siphonal margin. Some of the goniatites in their development pass through a stage resembling *Bactrites*.

Since the Ammonoids are extinct and their soft parts unknown it is impossible to determine what number of gills

they possessed; consequently their reference to the Tetrabranchia cannot be definitely established. As, however, the shell was external and agrees closely in structure with that of the Nautiloids, and the muscular impressions in the last chamber are similar to those found in *Nautilus*, we may regard the Ammonoids as closely allied to the Nautiloidea; this view of their relationship receives further support from the resemblance shown by the early Ammonoids (in their relatively simple sutures, backwardly-directed septal necks, the sinus at the external margin of the aperture, etc.) to the Nautiloids. The protoconch of the Ammonoids, however, differs from that of the Nautiloids and presents some resemblance to the protoconch of *Belemnites* and some other Dibranchs (page 299).

Clymenia (fig. 124). Shell discoidal; whorls numerous, more or less flattened, all visible, but each partly embracing the

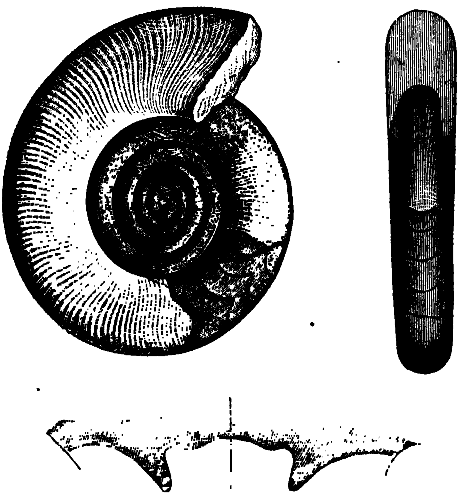


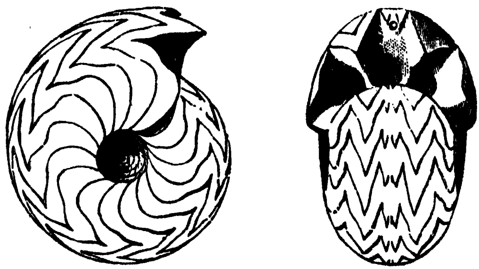
Fig. 124. *Clymenia* (*Oxyclymenia*) *undulata*, Upper Devonian. The lower figure shows the form of the suture. (After Nicholson.)

preceding one; body-chamber long, generally occupying three-quarters of the last whorl. Aperture with a sinus at the external margin. Sutures with a simple wavy or angular lateral lobe, a lobe at the internal margin (below the siphuncle) and a saddle at the external margin. Siphuncle on the internal margin; septal necks directed backwards. Surface usually ornamented with transverse striæ. Upper Devonian. Ex. *C. lævigata.* *Clymenia* is divided into *Cyrtoclymenia*, *Oxyclymenia*, *Cymaclymenia*, *Gonioclymenia*, etc.

Mimoceras[1]. Shell discoidal; the early whorls not in contact, the later ones contiguous. Siphuncle at the external margin[2]. Sutures very simple, concave on the sides of the whorls, with a funnel-shaped external lobe. Devonian. Ex. *M. compressum.*

Anarcestes. Shell with a wide umbilicus, and broad, rounded external margin. Body-chamber long; aperture with a deep external sinus. Sutures very simple; the external lobe funnel-shaped and not divided by a saddle; lateral lobe very flat. Septal necks long, directed backwards. Devonian. Ex. *A. plebeius* Lower and Middle Devonian.

Glyphioceras (fig. 125). Shell smooth or striated, whorls generally large and embracing, with rounded external margin; unbilicus small or absent. Septal necks short, directed backwards but



A B

Fig. 125. *Glyphioceras sphæricum*, from the Carboniferous Limestone. The shell has been dissolved exposing the sutures. A. Side view. B. View showing aperture with the siphuncle at the external (upper) margin. (From Woodward.) × ⅔.

[1] This and the four following, with several other genera, were formerly grouped together under the name *Goniatites*.

[2] In all the following genera the siphuncle has this position.

usually also with a small part projecting forwards. External lobe divided by a small saddle; external saddle narrow; lateral lobe angular and deep; lateral saddle broad, rounded, and undivided. Carboniferous. Ex. *G. sphæricum*, *G. crenistria*, Carboniferous Limestone.

Gastrioceras. Shell with longitudinal striæ, often with transverse ribs; with tubercles at the margin of the umbilicus. External margin broad, rounded. External lobe broad and deep, divided by a saddle; first lateral lobe deep, tongue-shaped, angular; second lateral lobe small, angular; saddles rounded. Carboniferous and Permo-Carboniferous. Ex. *G. carbonarium*, Coal Measures.

Prolecanites. Shell smooth or striated, flattened, with a large umbilicus. Lobes and saddles numerous. External lobe not divided; two or three lateral lobes, sharp; lateral saddles narrow and rounded. Devonian and Carboniferous. Ex. *P. compressus* (=*henslowi*), Carboniferous Limestone.

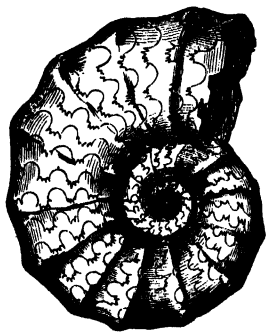


Fig. 126. *Ceratites nodosus*, from the Muschelkalk. The shell has been removed, exposing the sutures. × ⅔.

Ceratites (figs. 121 B, 126). Shell discoidal; on the sides are ribs which often bear tubercles near the umbilical and external margins; external margin broad, convex or flattened; umbilicus large; body-chamber short. Saddles rounded, lobes denticulate; external lobe broad and short. Trias, especially Muschelkalk. Ex. *C. nodosus*, Muschelkalk.

Trachyceras[1]. Shell flattened, highly ornamented with ribs which bear tubercles or spines arranged in spiral rows; at the

[1] This and the following genera, which are coiled in a plane spiral, with external siphuncle, and septal necks usually directed forwards in the adult, were formerly regarded as constituting a single genus—*Ammonites*. The genera now adopted are founded mainly on the form and ornamentation of the shell, the character of the sutures, and the length of the body-chamber.

external margin is a groove; umbilicus generally small. Body-chamber short. Sutures simple, lobes and saddles toothed. Trias. Ex. *T. aon.*

Arcestes. Shell smooth or striated, nearly globular, with thick whorls; umbilicus small or absent; aperture without lateral projections; body-chamber very long. Lobes and saddles numerous and foliaceous, arranged in a straight row and gradually decreasing in size from the external to the internal margin; there are two lateral lobes and many auxiliary lobes; saddles with narrow stems and fine branches. Trias. Ex. *A. intus-labiatus.*

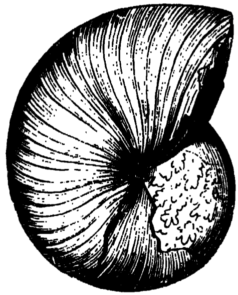


Fig. 127. *Phylloceras heterophyllum*, from the Lias. A part of the shell has been removed to expose the sutures. × ½.

Phylloceras (figs. 127, 128). Shell smooth or with fine striæ or gentle folds, never with tubercles; external margin rounded; umbilicus very small or absent. Saddles and lobes numerous; saddles divided, the extremities being rounded; auxiliary lobes numerous. Jurassic to Cretaceous. Ex. *P. heterophyllum*, Upper Lias.

Fig. 128. Suture line of *Phylloceras heterophyllum*, from the Lias. The arrow indicates the position of the siphuncle and points towards the aperture of the shell. (From Woodward.) Natural size.

Lytoceras (fig. 129). Shell ornamented with transverse ribs, and often with laminar projections (varices) placed at intervals. Whorls rounded, and only slightly or not at all embracing; aperture usually simple. Suture-line deeply and finely divided, consisting of an external lobe, two lateral lobes, and a narrow internal lobe; of an external saddle and two lateral saddles. Lateral lobes and saddles

nearly symmetrically divided. Lias to Cretaceous. Ex. *L. fimbriatum*, Middle Lias.

Hamites. Shell bent upon itself three times, the parts not in contact; body-chamber long. Suture-line similar to *Lytoceras*, with the lateral lobes deeply divided. Surface smooth, or ornamented with ribs, tubercles, or spines. Lower Greensand to Chalk. Ex. *H. maximus*, Gault.

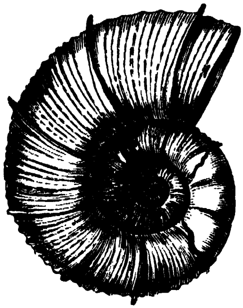


Fig. 129. *Lytoceras fimbriatum*, from the Middle Lias. × ½.

Macroscaphites (fig. 130). Similar to *Lytoceras*. Discoidal; the last whorl produced and then bent back in the form of a hook. Lower Cretaceous. Ex. *M. ivani*, *M. gigas*.

Turrilites. Shell helicoid-spiral, turreted, usually sinistral, all the whorls in contact. Sutures similar to *Lytoceras*. Surface ornamented with transverse ribs or tubercles. Gault to Chalk. Ex. *T. costatus*, Chalk.

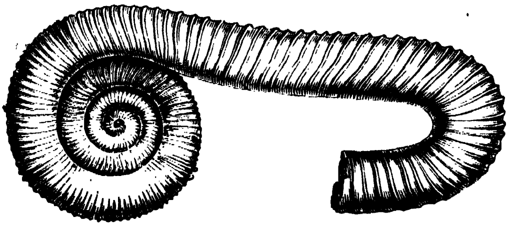


Fig. 130. *Macroscaphites ivani*, from the Lower Cretaceous. × ⅛.

Baculites. Shell straight (except a small spiral part at the apex, which is the first-formed part of the shell), elongate-conical, elliptical in section; body-chamber large, aperture produced at the outer (siphonal) margin. Sutures with the lobes symmetrically divided. Upper Cretaceous. Ex. *B. vertebralis* (=*faujasi*), Chalk.

Psiloceras. Shell discoidal, umbilicus large; whorls increasing in size very slowly, external border rounded or with a very small keel; surface smooth or striated, occasionally with ribs.

Body-chamber large. Sutures not much divided. Lower Lias. Ex. *P. planorbis.*

Arietites. Shell discoidal, umbilicus large; whorls numerous, only slightly embracing, with the external border flattened and provided with a keel having a groove on each side of it. Surface with strong simple ribs, which are straight or bent near the margin, and may bear tubercles. Body-chamber occupying from one to one and a quarter whorls. Sutures much divided, with two lateral lobes and one auxiliary lobe. Lower Lias. Ex. *A. bisulcatus.*

Schlotheimia. Shell flat, discoidal, umbilicus usually large. Ribs strong, curved, often bifurcated in the adult, bending forward at the external margin, where they meet at an angle, but are often interrupted by a slight furrow or smooth band at the margin. Sutures deeply divided; superior lateral lobe generally deeper than the external lobe; three or four auxiliary lobes. Lower Lias. Ex. *S. angulata.*

Ægoceras (fig. 131). Shell discoidal, with a large umbilicus; whorls rounded, without a keel, ornamented with simple ribs which are continuous over the external margin. Lobes much divided; superior lateral lobe larger than the others. Lias. Ex. *Æ. capricornus.*

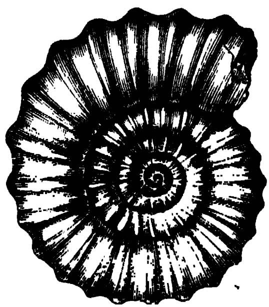


Fig. 131. *Ægoceras (Amblycoceras) capricornus*, from the Middle Lias. × ½.

Oxynoticeras. Shell much flattened; umbilicus small; external margin sharp or kneeled; surface smooth or striated. Sutures not deeply divided; external saddle large, divided; auxiliary lobes present. Lias to Inferior Oolite. Ex. *O. oxynotum*, Lower Lias.

Amaltheus. Shell flattened; with a keel, which is usually toothed but sometimes sharp; umbilicus generally small; surface smooth, or with striæ, or simple or spiny ribs. Aperture with a long process at the external margin. Lobes and saddles deep and much divided, with several auxiliary lobes. Jurassic. Ex. *A. margaritatus*, Middle Lias.

Harpoceras (fig. 132). Shell flattened, with a prominent even keel having a shallow furrow on each side; umbilicus small or of moderate size. Sides of shell with sickle-shaped undivided ribs. Aperture with projections. Sutures strongly divided; superior lateral lobe deep. Lias. Ex. *H. serpentinum*, Upper Lias.

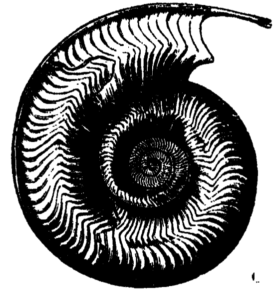


Fig. 132. *Harpoceras serpentinum*, from the Upper Lias. × ⅛.

Hildoceras. Similar to the last. Whorls low, subquadrate in section, with broad external margin and usually a deep furrow on each side of the keel. Umbilicus wide. Ribs distinctly sickle-shaped in most cases. Upper Lias and base of Inferior Oolite. Ex. *H. bifrons*.

Dactylioceras. Whorls numerous, only a little embracing, without a keel; umbilicus large. Ribs numerous, at first straight, afterwards bifurcating, continued over the external margin; without tubercles. Body-chamber long. Sutures moderately divided; external lobe larger than the superior lateral. Upper Lias and lower part of Inferior Oolite. Ex. *D. commune*, Upper Lias.

Stepheoceras (=*Stephanoceras*) (fig. 133). Whorls thicker than high, external margin rounded, without a keel. Umbilicus

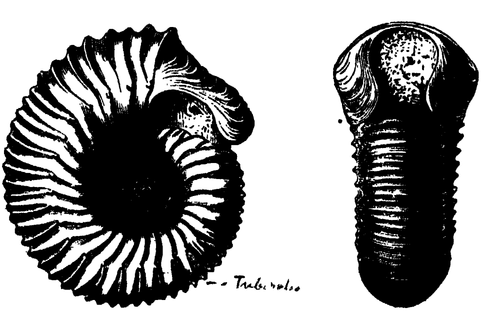


Fig. 133. ***Stepheoceras (Normannites) braikenridgei*, from the Inferior Oolite. × ⅜.**

large. Surface with straight ribs, which bifurcate on the sides of the whorls and often bear tubercles where they bifurcate. Body-chamber long. Aperture often with lobes. Sutures deeply divided; external lobe large; inferior lateral lobe and auxiliary lobes small. Inferior Oolite to Oxfordian. Ex. *S. humphriesianum*, Inferior Oolite.

Macrocephalites. Shell without a keel, whorls largely embracing, external margin rounded, umbilicus small. Ribs numerous, dividing near the umbilicus, continued over the external margin, and without tubercles. Aperture without lobes. Sutures deeply divided, with auxiliary lobes. Great Oolite to Kellaways Rock. Ex. *M. macrocephalus*, Cornbrash.

Cardioceras (fig. 134). Shell flattened; whorls considerably embracing, with strong curved ribs which bifurcate, and bending forward near the external edge join the notched keel; short ribs often intercalated on the external part. Lobes and saddles moderately divided; two short lateral lobes, and two or three auxiliary lobes; internal lobe with a single point. Kellaways Rock and Oxfordian. Ex. *C. cordatum*, Oxfordian.

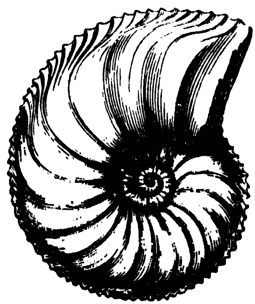


Fig. 134. *Cardioceras cordatum*, from the Oxfordian. $\times \frac{5}{6}$.

Perisphinctes. Shell discoidal, external margin rounded; umbilicus generally large. Ribs straight, continuous, bifurcating once or more near the external border. Constrictions are often present at intervals on the whorls. Sutures much divided; external and superior lateral lobes large. Inferior Oolite to Cretaceous. Ex. *P. plicatilis*, Corallian.

Peltoceras. Umbilicus large; whorls generally quadrilateral, with broad external margin, the inner whorls with numerous continuous ribs, most of which divide near the external margin, across which they extend; the ribs on the later whorls with two rows of tubercles on the sides, one near the outer, the other near the inner margin. Sutures moderately divided, with large external saddle. Kellaways Rock and Oxfordian. Ex. *P. athleta*.

Parkinsonia (fig. 121 A). Shell discoidal, umbilicus large; ribs nearly straight, sharp, bifurcating near the external border, but interrupted at the external margin by a groove. Aperture with processes from the sides. Body-chamber short. Sutures much divided; external and superior lateral lobes deep; saddles broad. Inferior Oolite. Ex. *P. parkinsoni.*

Cosmoceras. Shell flattened; umbilicus moderately large. Ribs numerous, bifurcating at the middle of the sides of the shell, where there is generally a row of tubercles, and ending in a tubercle or spine at the external margin; sometimes with tubercles at the edge of the umbilicus. Body-chamber very short. Aperture with long lateral lobes. Sutures much divided; the external lobe much shorter than the superior lateral lobe; there are several auxiliary lobes. Middle Lias to Oxfordian. Ex. *C. jason*, Oxfordian.

Hoplites. Shell flattened; umbilicus usually small. Ribs curved, bifurcating, and generally bearing a row of tubercles near the external margin and another near the umbilicus or at the middle of the sides; external margin flattened or deeply grooved. Sutures finely divided; many auxiliary lobes. Cretaceous. Ex. *H. splendens*, *H. interruptus*, Gault.

Acanthoceras. Whorls thick; umbilicus large; ribs simple or bifurcated, with rows of tubercles at the sides and margin; external margin broad with a median row of tubercles. Saddles broad. Chalk. Ex. *A. rhotomagense*, Lower Chalk.

Crioceras. Shell coiled in a plane spiral; the whorls not in contact. Surface ornamented with ribs which in some cases bifurcate and often bear tubercles and spines. Sutures with four lobes. Jurassic to Chalk. Ex. *C. ellipticum*, Chalk.

Ancyloceras. Like *Crioceras*, but the last whorl is produced in a straight line and then bent back in the form of a hook. Cretaceous. Ex. *A. spinigerum*, Gault.

Scaphites. Shell coiled in a plane spiral; the whorls in contact and embracing, except the last, which is free from the spiral and then recurved in the form of a hook. Body-chamber long. Surface ornamented with bifurcated ribs which often bear tubercles. Sutures generally much divided, with several auxiliary lobes. Upper Cretaceous. Ex. *S. æqualis*, Lower Chalk.

Schlœnbachia. Shell with an umbilicus; external margin broad with a smooth keel; surface with strong ribs, which are slightly curved forwards and often bear tubercles. External and superior lateral saddles broad; one auxiliary lobe. Cretaceous. Ex. *S. varians*, Lower Chalk.

ORDER II. DIBRANCHIA

The Dibranchia are represented at the present day by the cuttle-fishes, the squids, the calamaries, octopuses, paper-nautilus, etc.; they are of much less importance geologically than the Nautiloids and Ammonoids, the only really common fossil forms being *Belemnites* and its allies. Some of the modern cuttle-fishes attain a length of forty feet or more.

The Dibranchia (fig. 115) have a sac-like or elongated body, and possess one pair of gills only, and one pair of auricles. The number of arms is limited to eight or ten; and on the inner side—that facing the mouth—they are provided with rows of sucking-discs, which sometimes possess horny hooks. The jaws are not calcified, and are consequently seldom preserved in fossil specimens. An ink-sac is always present, and is sometimes found fossil. The funnel is in the form of a complete tube. The eyes are highly developed.

A shell is absent in some forms; when present it is (except in *Argonauta*) internal, being covered by folds of the mantle, and may be either horny or calcareous. In some cases (*Sepia*) it has the form of an oval flattened body, known as the *cuttle-bone*, which is composed mainly of laminated calcareous material with spaces between the laminæ. In the squids the shell is lamellar in form and consists of horny material; it is termed the *pen* or *gladius*. The shell in the cuttle-fishes and squids is placed on the

antero-dorsal side of the body in a sac formed by the mantle. In *Spirula* the shell resembles that of a Tetrabranch, but is internal, being almost entirely covered by the mantle; it is situated at the dorsal end of the body, and consists of a tube coiled in a plane spiral and divided into chambers by septa, which are traversed by a siphuncle placed near the inner margin; the whorls are not in contact, and a calcareous protoconch is present. The shell in the paper-nautilus (*Argonauta*) is of quite a different nature to that found in other Dibranchs; it is external and spiral, but not chambered, and is without muscular attachments; it is secreted by the terminal portions of the two anterior arms, and is found only in the female, serving for the reception of the eggs.

The Dibranchia are divided into two sub-orders:—(1) the Decapoda, (2) the Octopoda.

SUB-ORDER 1. DECAPODA

There are ten arms, eight of equal length and two longer than the others; the latter can be more or less completely retracted within pits. The free ends of the arms are swollen and suckers are usually borne on those ends only. The suckers are stalked and are provided with a horny ring. An internal shell is always present.

Belemnites (figs. 135—138). The shell consists of three parts—the guard (fig. 135, *a*), the phragmocone (*b*), and the pro-ostracum (fig. 136, *d*).

The *guard* is solid and is much more commonly preserved than the other parts; it varies considerably in shape and size, being cylindrical, fusiform, conical, etc. The end which was directed away from the mouth is always pointed, and at the other end there is a conical cavity or alveolus. The guard varies in length from one to fifteen inches. When sliced transversely or longitudinally it is seen to be formed of a number of layers (growth-layers) arranged concentrically

around an axial line, which is not quite central but is placed nearer the under surface; it is around this line that the first layers were secreted; the layers become somewhat thicker towards the pointed end and thinner towards the broad end of the guard. Each layer is formed of minute prisms of calcite, which are placed perpendicular

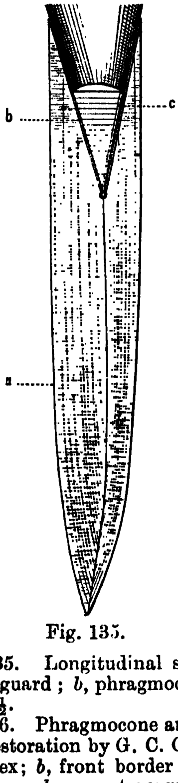


Fig. 135.

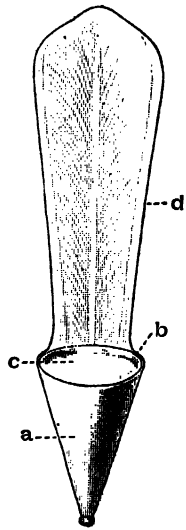


Fig. 136.

Fig. 135. Longitudinal section of *Belemnites*, from the Oxford Clay. *a*, guard; *b*, phragmocone with protoconch at the apex; *c*, siphuncle. $\times \frac{1}{2}$.

Fig. 136. Phragmocone and pro-ostracum of *Belemnites*, from the Lias. Restoration by G. C. Crick. *a*, phragmocone with protoconch at the apex; *b*, front border of phragmocone; *c*, last septum of phragmocone; *d*, pro-ostracum. $\times \frac{2}{3}$.

to the axial line, thus producing a radiating fibrous appearance in cross-sections. The surface of the guard is sometimes smooth, or it may be granular, or furnished with ramifying vascular impressions; in some species there is a longitudinal groove on the under surface.

The *phragmocone* (figs. 135, *b*; 136, *a*) is a hollow cone, part of which fits into the alveolus at the broad end of the guard; it is divided into chambers by septa which are concave in front; a siphuncle (fig. 135, *c*) traverses the chambers at the under margin; at the pointed end of the phragmocone is a globular or ovoid protoconch formed of calcareous material (figs. 135, 136). The

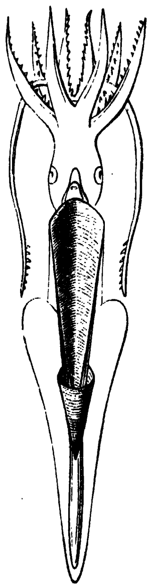


Fig. 137.

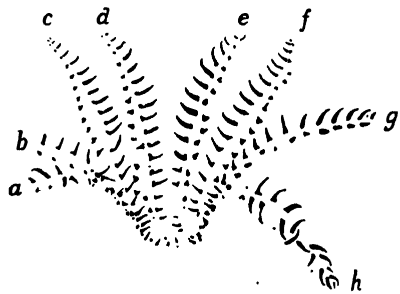


Fig. 138.

Fig. 137. D'Orbigny's restoration of a Belemnite (under surface), showing the probable positions of the guard, the phragmocone, and the pro-ostracum.

Fig. 138. *Belemnites*. Lias, Lyme Regis. Original in the Sedgwick Museum, Cambridge. Showing hooks indicating the presence of eight arms (*a*—*h*). $\times \frac{3}{4}$.

phragmocone is homologous with the entire shell of a Nautiloid or an Ammonoid; in its conical form and simple sutures it resembles *Orthoceras*, but the calcareous protoconch and slender marginal siphuncle seems to connect it more closely with the Ammonoids. The wall of the phragmocone (sometimes termed the *conotheca*) is

very thin, and in well-preserved specimens the upper part is found to be produced in front into a large laminar expansion (fig. 136, *d*); this prolongation is known as the *pro-ostracum*, and corresponds to the 'pen' of the squids. The head of the Belemnite was immediately in front of the pro-ostracum. The suckers on the arms were provided with horny hooks, which are sometimes preserved fossil (fig. 138); there was a double row of hooks on each arm, but only eight double rows have yet been found in any specimen; two other arms, with or without hooks, may have been present. The ink-sac and mandibles have also been found in some specimens. The probable positions of the guard, phragmocone and pro-ostracum in the body of the Belemnite are shown in fig. 137, from which it is seen that the guard formed a relatively small part of the entire length of the animal. The 'genus' *Belemnites* is founded mainly on the characters of the guard, and includes an enormous number of species. Probably if the soft parts were known, they would show such differences as to indicate a number of distinct genera. Lower Lias to Upper Cretaceous. Ex. *B. acutus*, Lias; *B. oweni*, Oxford Clay, etc.; *B. hastatus*, Oxford Clay.

Belosepia, found in the Eocene, is related to *Belemnites*, but the guard is considerably reduced in size, and the septa curve forward from the broad siphuncle towards the pro-ostracum. *Spirulirostra*, from the Eocene and Miocene, is another allied form; it possesses a small guard ending in a point, and the first part of the phragmocone is coiled. In *Sepia* (Eocene to Recent), the laminæ which form the main part of the shell, are believed to represent the septa of the phragmocone, whilst the guard is reduced to a small pointed process (or mucro) at the end. *Spirula* has not been found fossil.

Belemnitella. Similar to *Belemnites*. Guard cylindrical, with a slit at the under side of the alveolus. Distinct vascular impressions on the under surface of the guard. Upper Chalk. Ex. *B. mucronata*.

Actinocamax (= *Atractilites*). Similar to Belemnites. Front part of guard either conical or broadly funnel-shaped, and either in contact with the protoconch only or surrounding only the apical part of the phragmocone. Front part of guard often fragile and foliaceous owing to imperfect calcification. Chalk. Ex. *A. plenus*, Lower Chalk; *A. quadratus*, Upper Chalk.

Aulacoceras. Similar to *Belemnites.* Guard relatively short, with a groove extending down each side. Phragmocone much longer than the guard, with siphuncle at the margin, and septa rather widely separated; surface of phragmocone with longitudinal lines. Pro-ostracum unknown. Upper Trias. Ex. *A. reticulatum.*

Belemnoteuthis. Guard much reduced, forming a thin layer over the phragmocone, with a groove on the upper side starting from the pointed end. Phragmocone broad, with numerous septa, a marginal siphuncle, and septal necks. Pro-ostracum relatively small, seldom preserved. Ten arms bearing hooks. The ink-sac is sometimes found. Chiefly Oxfordian. Ex. *B. antiqua.*

SUB-ORDER 2. OCTOPODA

There are eight arms only; the suckers are sessile and possess no horny ring. The shell is rudimentary or absent. *Octopus* and *Argonauta* are well-known examples of this group. The Octopoda, as might be expected from the general absence of a shell, are very poorly represented in the fossil state; the earliest known form is *Palæoctopus* from the Chalk of Lebanon. *Argonauta* has been found in the Pliocene Beds.

Distribution of the Cephalopoda

Nautiloidea. At the present day the Nautiloidea are represented by only four species of *Nautilus,* which are found in the Indian Ocean and the East Indian Archipelago (from Sumatra to Fiji). *Nautilus* lives in fairly shallow water, either crawling on the sea bottom by means of its tentacles or swimming.

This group appears much earlier in the geological series than either the Ammonoidea or the Dibranchia. The early forms are either straight or slightly curved, subsequently genera with spiral shells appear; the former predominate

in the Lower Palæozoic, but become less important in the Upper Palæozoic where the plane spiral forms increase in numbers. Primitive Nautiloids (*Volborthella*) are found in the Lower Cambrian; and forms of the type of *Orthoceras* and *Cyrtoceras* appear in the Upper Cambrian (Tremadoc Beds). In the Ordovician the Nautiloidea are very much better represented than in the Cambrian, and the group attains its maximum development in the Silurian, where the number of species is very great; it decreases slightly in importance in the Devonian and Carboniferous, and is but poorly represented in the Permian. The only genus which extends beyond the limit of the Palæozoic period is *Orthoceras*, which is found in the Trias. *Nautilus* occurs first in the Trias and is abundant in the Jurassic and Cretaceous; in the Tertiary it is relatively rare. *Aturia* appears in the Eocene and Miocene.

Ammonoidea. The geological range of the Ammonoidea is shorter than that of the Nautiloidea. The earliest representatives of this sub-order are found in the Devonian; the latest in the Chalk. The group is especially abundant in the Mesozoic formations. *Clymenia* is limited to the Upper Devonian; goniatites also occur in the rocks of that system, but are more numerous in the Carboniferous—*Glyphioceras* and *Gastrioceras* being especially characteristic of the latter. Ammonites are found in Permian deposits, and primitive forms appear even as early as the Carboniferous; throughout the Mesozoic rocks they are extremely abundant, attaining their maximum in the Lias. In the Cretaceous there is a remarkable development of more or less completely uncoiled Ammonoids, *e.g.*, *Hamites*, *Macroscaphites* (fig. 130), *Baculites*, *Crioceras* and *Scaphites*; and there is evidence showing that, in most cases, these 'genera' include species which have descended from more

than one genus of ammonites. The abrupt disappearance of the Ammonoidea at the end of the Cretaceous period is remarkable.

Dibranchia. The Dibranchia are more numerous and more varied in existing seas than they were at any former period. Some forms are pelagic, others abyssal, but the larger number are found in littoral regions and are distributed in provinces similar to those of other molluscs (p. 268); typical littoral genera are *Octopus, Sepia* and *Loligo.*

The Dibranchia are unknown in the Palæozoic formations, the earliest examples (*Aulacoceras, Phragmoteuthis*) appearing in the Trias. *Belemnites* is the chief form in the Jurassic and Cretaceous, and is especially abundant in the clayey beds. *Geoteuthis* occurs in the Lias; and *Belemnoteuthis, Plesioteuthis,* etc. in the Upper Jurassic. *Belemnitella* is limited to the Upper Chalk. Dibranchs are relatively rare in the Eocene and Miocene; *Belemnites* is absent, but is represented by *Belosepia* and *Spirulirostra.*

The principal genera of Cephalopoda are:

Cambrian. *Volborthella* in the Lower Cambrian; *Orthoceras* and *Cyrtoceras* in the Tremadoc Beds.

Ordovician. *Orthoceras, Cyrtoceras, Endoceras, Piloceras, Conoceras.*

Silurian. *Orthoceras, Cyrtoceras, Actinoceras, Gomphoceras, Phragmoceras, Ascoceras, Ophidioceras.*

Devonian. Nautiloidea :—*Orthoceras, Cyrtoceras.* Ammonoidea :—*Clymenia, Bactrites, Mimoceras, Anarcestes, Tornoceras, Gephyroceras.*

Carboniferous. Nautiloidea :—*Orthoceras, Cyrtoceras, Actinoceras, Poterioceras, Discites, Vestinautilus, Cœlonautilus, Pleuronautilus, Temnocheilus.* Ammonoidea :—*Glyphioceras, Gastrioceras, Prolecanites.*

Permian. Nautiloidea :—*Orthoceras*, *Temnocheilus*. Ammonoidea :—*Medlicottia*, *Cyclolobus*.

Trias. Nautiloidea :—*Nautilus*, *Orthoceras*. Ammonoidea :—*Pinacoceras*, *Ceratites*, *Trachyceras*, *Ptychites*, *Arcestes*, *Cladiscites*, *Monophyllites*, *Rhacophyllites*. Dibranchia :—*Aulacoceras*, *Atractites*, *Phragmoteuthis*.

Lias. Nautiloidea :—*Nautilus*. Ammonoidea :—*Phylloceras*, *Lytoceras*, *Psiloceras*, *Arietites*, *Ægoceras*, *Liparoceras*, *Oxynoticeras*, *Amaltheus*, *Schlotheimia*, *Harpoceras*, *Hildoceras*, *Cœloceras*, *Dactylioceras*. Dibranchia :—*Belemnites*, *Xiphoteuthis*, *Geoteuthis*.

Oolites. Nautiloidea :—*Nautilus*. Ammonoidea :—*Ludwigia*, *Leioceras*, *Haploceras*, *Stepheoceras*, *Macrocephalites*, *Cardioceras*, *Quenstedtoceras*, *Perisphinctes*, *Peltoceras*, *Aspidoceras*, *Parkinsonia*, *Cosmoceras*. Dibranchia :—*Belemnites*, *Belemnoteuthis*, *Acanthoteuthis*.

Lower Cretaceous. Nautiloidea.—*Nautilus*. Ammonoidea :—*Macroscaphites*, *Hamites*, *Holcostephanus*, *Desmoceras*, *Parahoplites*, *Douvilleiceras*, *Crioceras*. Dibranchia :—*Belemnites*.

Upper Cretaceous. Nautiloidea :—*Nautilus*. Ammonoidea :—*Hamites*, *Turrilites*, *Baculites*, *Desmoceras*, *Pachydiscus*, *Hoplites*, *Acanthoceras*, *Scaphites*, *Schlœnbachia*. Dibranchia :—*Belemnites*, *Belemnitella*, *Actinocamax*.

Eocene. Nautiloidea :—*Nautilus*, *Aturia*. Dibranchia :—*Belosepia*, *Beloptera*, *Spirulirostra*.

PHYLUM ARTHROPODA

Classes.	*Sub-Classes.*	*Orders.*
1. Crustacea	1. Trilobita.	
	2. Branchiopoda.	
	3. Ostracoda.	
	4. Copepoda (not fossil).	
	5. Cirripedia.	
	6. Malacostraca	1. Leptostraca.
		2. Syncarida.
		3. Peracarida.
		4. Eucarida.
		5. Hoplocarida.
2. Onychophora (not fossil).		
3. Myriapoda.		
4. Insecta.		
5. Arachnida	1. Merostomata	1. Xiphosura.
		2. Eurypterida.
	2. Euarachnida	1. Scorpionida.
		2. Pedipalpi.
		3. Araneida.
		4. Pseudoscorpionida.
		5. Phalangida.
		6. Acarina.
		7. Anthracomarti.

The Arthropods have a bilaterally symmetrical body, formed of a series of segments (or somites), but the segments are not all alike, and some are fused together. Some, or all of the segments, bear a pair of jointed appendages or limbs, those near the mouth being modified to serve as jaws. A chitinous exoskeleton is always present,

and is often strengthened by the deposition of carbonate or phosphate of lime; between the segments the integument remains soft and flexible, so that movement of the parts of the body is rendered possible. A heart is found in most forms; it is placed dorsally, and is provided with paired slits, termed ostia. The body-cavity contains blood. In some forms respiration takes place by means of the general surface of the body; others are provided with special organs—gills (or branchiæ), tracheæ, or lung-books. The gills are generally thin projections of the skin borne by some of the appendages; the tracheæ are long, branching tubes, filled with air, which penetrate all parts of the body and open to the exterior; the lung-books are chambers containing leaf-like folds of the skin. The nervous system consists of a supra-œsophageal ganglion or brain, connected by a ring round the œsophagus with a ventral cord, usually provided with ganglia, and placed beneath the intestine. The sexes are separate in the majority of forms.

The Arthropoda are divided into the following Classes:—(1) Crustacea, (2) Onychophora, (3) Myriapoda, (4) Insecta, (5) Arachnida. The Onychophora include one genus only—*Peripatus*, which has not been found fossil.

CLASS I. CRUSTACEA

The Crustacea are mainly aquatic animals, and are abundant as fossils; they breathe generally by means of gills, but in some cases respiration takes place through the general surface of the body. The chitinous exoskeleton is frequently hardened by a calcareous deposit,—hence the name Crustacea. Segmentation is usually well marked, but in the Ostracoda is shown by the appendages only. The exoskeleton of a segment or somite consists of a dorsal

part, the *tergum*, and a ventral part, the *sternum*. In the higher Crustacea, three regions may be distinguished in the body:—the head, the thorax, and the abdomen; but in the lower forms the abdomen is often not clearly differentiated from the thorax. In the head there are five segments fused together, but externally these (except in Trilobites) are indicated only by the appendages. The number of segments in the trunk (thorax and abdomen) is variable in the lower Crustacea, but is constant in the Malacostraca. In many forms some or all of the segments of the thorax fuse with those of the head, forming a *cephalothorax*. In many Crustacea there is a dorsal shield or *carapace* which covers part, or sometimes the whole, of the body, and originates as an outgrowth from the posterior margin of the dorsal part of the head. The head usually bears five pairs of appendages, viz.:—two pairs of feelers (the antennules and antennæ), one of mandibles, and two of maxillæ; the first two pairs are in front of the mouth. The thorax is also provided with appendages, and often the abdomen too. The mandibles and maxillæ, and frequently some of the anterior thoracic appendages, serve as jaws. The Crustacean appendage is typically biramous, consisting of a basal part (the *protopodite*) bearing two branches—the inner called the *endopodite*, and the outer termed the *exopodite* (fig. 144 C). The protopodite usually consists of two segments—a proximal or *coxopodite*, and a distal or *basipodite*. In some cases the exopodite disappears and the limit becomes *uniramous*. The mouth is on the under surface of the head, and the anus is on the last segment (the telson) of the body. Eyes are generally present, commonly a pair of compound eyes, and sometimes a median simple eye; in many Crustacea the former are placed on movable stalks. The sexes are separate except

in most of the cirripedes and in some parasitic isopods. In the Malacostraca the genital apertures are on the sixth thoracic segment in the male, and on the eighth in the female; in the lower Crustacea (Entomostraca) the position of the apertures is variable.

In some Crustacea development is direct, that is to say, the young individual has the same form as the adult; but generally this is not the case, the young undergoing metamorphosis before reaching the adult stage. The two chief larval forms are known as the *nauplius* and the *zoœa.* In the nauplius the body is unsegmented, and possesses three pairs of appendages representing the two pairs of antennæ and the mandibles. In the zoœa stage some of the thoracic appendages are present also, and the abdomen is segmented but possesses no appendages.

The Crustacea are divided into six sub-classes:—(1) Trilobita, (2) Branchiopoda, (3) Ostracoda, (4) Copepoda, (5) Cirripedia, (6) Malacostraca. The Copepods are not definitely known as fossils.

The first five sub-classes are usually grouped together as the *Entomostraca,* but they differ considerably from one another and are not united by the possession of important features common to all. In comparison with the Malacostraca they are generally of simple organisation, usually with the number of segments in the trunk varying widely, and with the abdomen usually ending in a caudal fork; with the exception of the Trilobita they are generally of small size, and often without a clear differentiation of the trunk into thorax and abdomen. A median unpaired eye is usually present.

SUB-CLASS I. TRILOBITA

The Trilobites derive their name from the fact that the body is divided into three parts, by means of two furrows, which extend from the anterior to the posterior extremities; this trilobation is usually conspicuous, but in a few genera (*e.g. Homalonotus, Illænus*), it is indistinct or almost

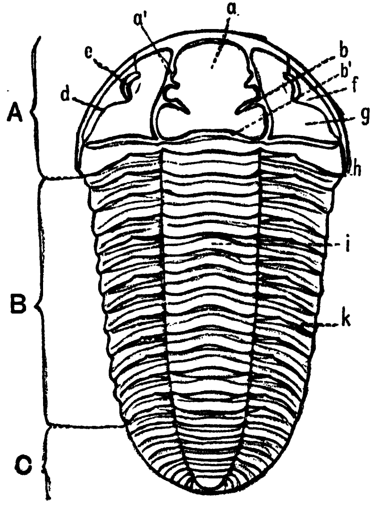


Fig. 139. *Calymene tuberculata*, from the Wenlock Limestone. Dorsal surface. A, head; B, thorax; C, pygidium or abdomen. *a*, glabella; *a'*, axial furrow; *b*, one of the glabella furrows; *b'*, neck-furrow, behind which is the neck-ring; *d*, facial suture; *e*, eye; *f*, free cheek; *g*, fixed cheek; *h*, genal angle; *i*, axis of thorax; *k*, pleura. Natural size.

obsolete. The body is oval in outline, and flattened from above downwards; it consists of the *head* (fig. 139 A), the *thorax* (B), and the *pygidium* or *abdomen* (C). The segments of the head and of the pygidium are fused together, but those of the thorax remain free. Traces of the alimentary

canal are sometimes found in the middle or axial part of the Trilobite.

The dorsal surface of the body is protected by a strong, calcareous exoskeleton. The part which covers the head is known as the *head-shield* or *cephalic shield*, and is usually semicircular or triangular in shape; in it may be distinguished a median and two lateral portions; the former is the more convex and is termed the *glabella* (*a*), the latter are the *cheeks*. The glabella is marked off from the cheeks by means of a furrow on each side, known as the *axial furrow* (*a′*). The form and relative size of the glabella vary in different genera; in some it extends quite to the anterior margin of the head-shield, in others only a part of the way (fig. 148); sometimes it is wider behind than in front; in other cases it is wider anteriorly, or it may be of uniform width throughout; its convexity also varies considerably—it may be nearly flat, but is sometimes pear-shaped or spheroidal. The segmentation of the head is indicated by transverse furrows on the glabella (*b*),—often three on each side; in some cases the opposite furrows from the two sides meet at the middle of the glabella. On the posterior part of the glabella there is another furrow, which extends quite across it and is continued on to the cheeks; this is known as the *neck-furrow* (*b′*), and the segment of the glabella behind it is the *neck-ring*. These furrows indicate the existence of five segments in the head. In primitive trilobites all the furrows are distinct, but in others some, especially the anterior furrows, become indistinct or obsolete.

The cheeks are more or less triangular in shape, and usually less convex than the glabella; they are frequently bordered by a flattened or concave margin which in *Trinucleus* is very broad and highly ornamented. The

posterior angles of the cheeks, known as the *genal angles* (*h*), may be rounded (*e.g. Calymene*), but are often pointed or produced into spines, the *genal spines* (*e.g. Paradoxides*, fig. 147). Each cheek is usually divided into two portions by a suture (the *facial suture*, *d*); the inner part—that between the facial suture and the glabella—is termed the *fixed cheek* (*g*) and is immovable; the outer part, known as the *free cheek* (*f*), is slightly movable on the fixed cheek. The course of the facial suture varies in different forms: it may commence on the posterior border inside the genal angle (fig. 150), or at or near the genal angle (*h*), or on the lateral border in front of the genal angle (fig. 151); it passes inwards to the eye and then bends forwards, and may be continuous with the suture of the other cheek in front of the glabella, or it may cut the anterior margin of the head-shield, in which case it is sometimes united with the suture of the other side on the inferior surface of the head (fig. 141, *d*). When the sutures are continuous in front of the glabella it is evident that the cheeks will also be continuous. Since the position of the facial suture varies in different genera the relative sizes of the fixed and free cheeks will obviously vary too; thus in *Illænus* the free cheek is very narrow, in *Phillipsia* very broad. Owing to the fusion of the fixed and free cheeks the facial suture is sometimes absent *e.g.* some species of *Acidaspis*; this is probably also the case in *Agnostus, Microdiscus* and a few other genera.

The compound eyes (fig. 139, *e*) are on the upper surface of the head, one on each free cheek in the angle made by the facial suture; they are more or less conical with the summit truncated or rounded, and with the visual surface on the external part. The eyes usually consist of a large number of lenses—in *Remopleurides* the number is stated

to be 15,000. Usually the lenses are biconvex or globular and adjacent to one another, but in *Phacops* and its allies the eyes are more highly developed, the lenses being separated by portions of the cephalic shield so that each appears to rest in a separate socket. The eye is entirely on the free cheek, but rests on a lobe or buttress on the adjacent part of the fixed cheek. In a few Trilobites the eyes appear to be of a simpler type; for example, in *Harpes* each eye usually consists of two or three lenses only, and in some species of *Trinucleus* of a single lens; but it is probable that in such cases the eye is merely a degenerate form of compound eye. In a few Trilobites (*Agnostus, Microdiscus, Ampyx, Conocoryphe*, some species of *Acidaspis*, etc.) eyes are absent; in such cases it is probable that the visual organs have been lost through disuse, just as is the case with some Crustacea at the present day which live at great depths in the sea or in other places where no light can penetrate. When eyes are absent the facial sutures also are usually wanting. In *Æglina* (fig. 140) the eyes are unusually large, occupying the greater part of the free cheeks, and sometimes extending on to the ventral surface; it is probable that this Trilobite was a pelagic animal which swam near the surface of the sea at night, but sank to considerable depths, where there was but little light, during the daytime. In many of the Cambrian Trilobites the eye itself is not found, but since the eye-lobe is present it is reasonable to infer that it supported the visual organ, and that the absence of the latter is due to imperfect preservation; this view is rendered more probable by the

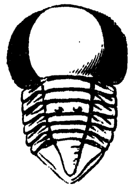


Fig. 140. *Æglina binodosa*, Arenig Beds. Natural size.

recent discovery of the surface of the eye in a specimen of *Olenellus* from the Lower Cambrian. In many Cambrian and some few later Trilobites a thread-like ridge, called the *eye-line*, extends from the compound eye to the glabella (fig. 152, *o*—*n*).

In some Trilobites a small tubercle-like projection is found on the middle line of the front part of the glabella; this has been shown to be a visual organ and to possess a structure similar to that seen in the median unpaired eye of the Branchiopods and Ostracods.

The head-shield is continued on the under surface of the head as a reflexed border or marginal rim (fig. 141, *b*); sometimes the facial sutures (*c*) are continued across this border, and they may be joined by a transverse suture (*d*). Attached to the border in the median line is a plate (*a*), usually oval or shield-shaped, situated in front of and below the mouth and known as the *hypostome or labrum* (fig. 142). Just behind the mouth is the small lower lip-plate or *metastoma* (fig. 144 A, *m*), which, up to the present time, has been found in *Triarthrus* only.

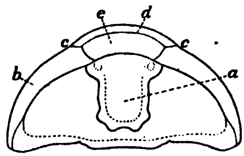


Fig. 141. *Calymene tuberculata*, Silurian. Ventral surface of head. *a*, hypostome; *b*, marginal rim; *c*, facial suture; *d*, transverse suture; *e*, rostral plate. (After Barrande.) Natural size.

In many Trilobites a small oval or elliptical area, sometimes slightly raised like a tubercle, in other cases depressed, is found on each side of the hypostome just behind the middle of its outer surface (fig. 142); these *maculæ* are sometimes entirely smooth, but in other cases a part, or the whole of the surface, shows a structure similar

to that of the compound eyes on the dorsal surface of the head, and such were probably visual organs. Maculæ are not known to occur in any other Crustacea.

The thorax (fig. 139 B) consists of a series of segments, which vary in number from two to twenty-nine, and are movable upon one another, in some cases sufficiently to enable the animal to roll itself up like a woodlouse. Each segment is divided into a median and two lateral parts by means of two furrows. The median or axial part is more convex than the lateral, and forms the axis (*i*), the lateral parts being known as the *pleuræ* (*k*). The anterior part (fig. 143, *c*) of the axis of each segment is not visible when the animal is unrolled, since it bends down and is overlapped by the preceding segment, for which it forms an articular surface. The pleuræ in some genera possess a longitudinal ridge, in others a groove (*h*), or both ridge and groove may occur; a few forms have plane pleuræ. Each pleura, at some distance from the axis, is curved downwards and usually also backwards; the point where this curvature occurs is known as the fulcrum (*e*); sometimes the outer part of each pleura overlaps the anterior part of the succeeding one, and then the front part of the pleura beyond the fulcrum may be smooth and flattened so as to form an articulating surface or *facet* (*f*). The terminations of the pleuræ are in some cases rounded (fig. 143), in others pointed or produced into spines (fig. 147).

Fig. 142. Hypostome of *Asaphus tyrannus*, from the Llandeilo Beds. Reduced.

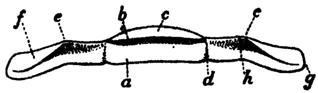


Fig. 143. Dorsal surface of a thoracic segment of *Asaphus expansus*. *a*, ring of axis; *b*, groove; *c*, articular portion; *d*, furrow between axis and pleura; *d—g*, pleura; *e*, fulcrum; *f*, facet; *h*, groove on pleura.

The pygidium or abdomen (fig. 139 C) is commonly triangular or semicircular in shape, and is formed of a variable number of segments, which are similar to those of the thorax but are fused together and immovable; on the dorsal surface the segmentation is shown by grooves only. The pygidium, like the thorax, is divided into a median part or axis, and lateral portions. The axis may reach quite to the posterior extremity or only part of the way, and it tapers more rapidly than the axis of the thorax; in *Bronteus* it is very short. The margin of the pygidium may be even or entire, or may be provided with a posterior spine or with lateral spines. This margin is bent under so as to form a border on the ventral surface similar to that on the ventral surface of the head.

For a long time the appendages of the Trilobites were unknown. In the great majority of specimens, when the under surface is exposed, the only parts which are found to be preserved are the hypostome and the reflexed borders of the dorsal exoskeleton. But in rolled-up specimens of *Calymene* and *Cheirurus*, Walcott showed, by means of thin sections, that jointed appendages are present on the head, thorax and pygidium, and that the ventral surface of the body is formed of a thin, uncalcified cuticle, strengthened by transverse arches.

More recently specimens in which the body is not rolled up, showing clearly the ventral surface with the appendages, have been obtained from the Utica Slate (Ordovician) near Rome (New York) and from the Middle Cambrian deposits of British Columbia. The most important of these belong to the genus *Triarthrus* from the Utica Slate (fig. 144). Each segment of the body, excluding the last (or anal), is found to bear one pair of appendages, which, with the exception of the first, are biramous. On

the head there are five pairs of appendages. The *first* are the long antennæ which are attached on each side of the hypostome (*h*) and consist of a large basal joint bearing a flagellum formed of numerous short conical joints; these appear to be the only appendages in front of the mouth, and are considered by Beecher to represent the antennules (first pair of antennæ) of other Crustacea. The remaining four pairs of appendages of the head are biramous and all appear to have nearly the same form but increase in size backwards; the *second* pair are considered to represent the antennæ, the *third* the mandibles, and the *fourth* and *fifth*

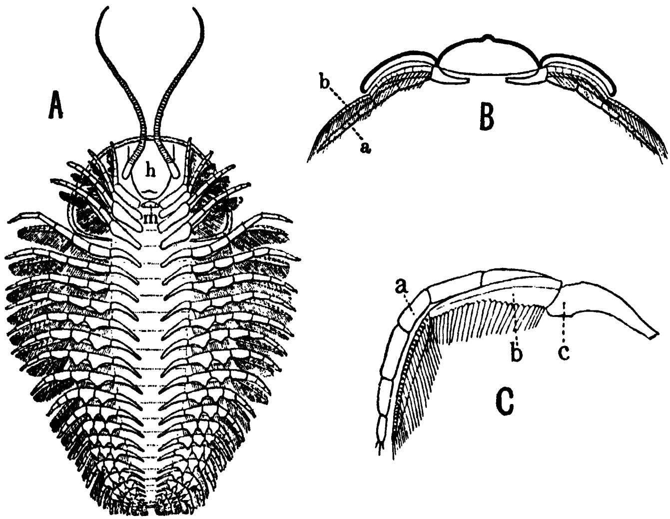


Fig. 144. *Triarthrus becki*, from the Utica Slate (Ordovician) near Rome, New York. (After Beecher.)

A. View of the ventral surface showing appendages, etc. *h*, hypostome; *m*, metastoma. $\times \frac{2}{3}$.

B. Diagrammatic section through the second thoracic segment. *a*, endopodite; *b*, exopodite.

C. Dorsal view of second thoracic leg. *a*, endopodite; *b*, exopodite; *c*, protopodite with gnathobase. Enlarged.

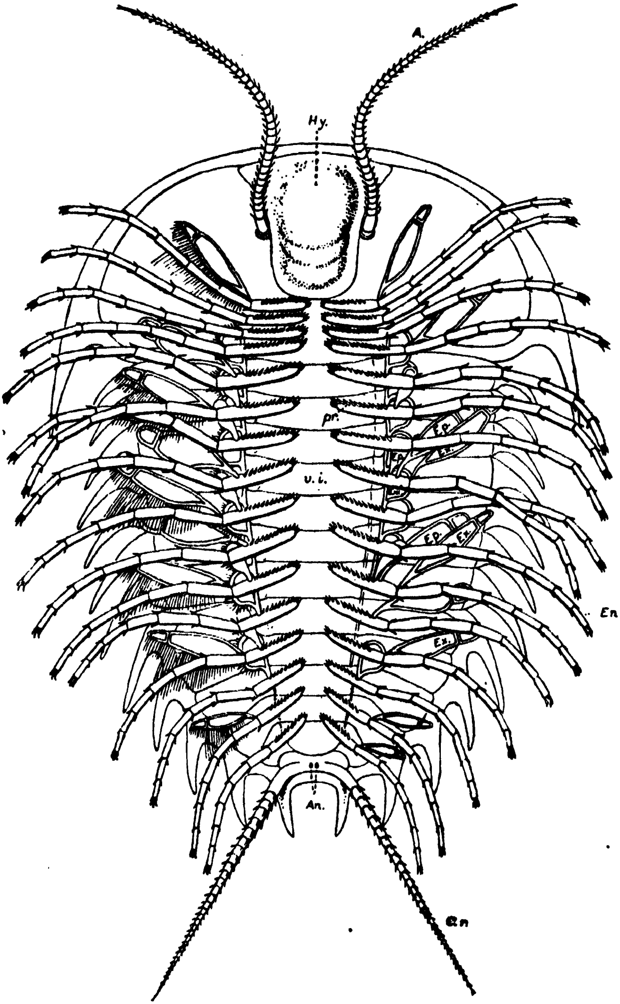


Fig. 144 A. *Neolenus serratus*, Middle Cambrian. Restoration of ventral surface. *A*, antennules; *An*, anus; *C.r.* caudal rami; *En*, endopodite; *Ep*, epipodite; *Ex*, exopodite; *Hy*, hypostome; *pr*, protopodite; *v.i.* ventral integument. The setæ have been omitted from the appendages on the right hand side of the figure. (After Walcott). $\times \frac{3}{4}$.

pairs the maxillæ of other Crustacea. Each maxilla consists of a large basal joint (the *protopodite*) which bears a stout *endopodite* and a slender *exopodite*; the latter carries a row of hairs or *setæ*; the inner edge of the protopodite is toothed and served as a jaw (gnathobase); whilst the endopodite and exopodite assisted in locomotion.

The appendages of the thorax are long, but gradually decrease in size backwards, and consist of a protopodite (fig. 144 C, *c*) bearing the endopodite (*a*) and the exopodite (*b*) which are of nearly equal length. The endopodite is formed of six joints, and probably served as a swimming organ. The exopodite consists of a long basal joint followed by a part consisting of numerous short joints; it bears setæ along its posterior edge and was probably adapted for crawling. The inner prolongations of the protopodites served as gnathobases. The limbs in each pair are widely separated, and in each segment the ventral cuticle between their bases is strengthened by a median longitudinal ridge and one or two oblique ridges on each side. On the posterior part of the thorax some of the joints of the endopodites become flattened.

The appendages of the pygidium are similar to those on the posterior part of the thorax, but are more distinctly leaf-like owing to the flattening and expansion of the first segments of the endopodite which bear setæ; the exopodite is slender. The anal opening is on the last segment (or telson) near the end of the pygidium.

In specimens of *Neolenus* from the Middle Cambrian of British Columbia, Walcott has discovered the caudal fork; it consists of a pair of jointed filaments coming off from the end of the pygidium (fig. 144 A, *C.r*). Leaf-like epipodites (*Ep*) have also been found in *Neolenus*; each consists of two joints and is attached to the protopodite.

In some fine-grained deposits, especially in the Lower Palæozoic rocks of Bohemia, the larval forms of Trilobites are found well preserved, and by obtaining specimens of different ages it is possible to trace out the changes which occurred in the development of the individual. In the earliest stage (fig. 145 A), called the *protaspis* by Beecher, the body is discoid or ovate in form, and consists of a large cephalic region and a small pygidial part; the axis is distinct, and is marked by furrows; eyes, when present, are at or near the outer front margins of the shield (fig. 145 E), and the free cheek, if present, is narrow (G). The

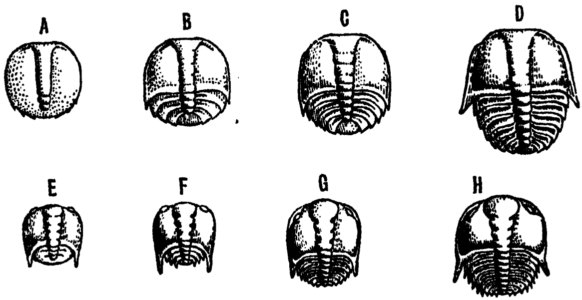


Fig. 145. Development of Trilobites. (After Barrande.)

A—D. *Sao hirsuta*, Cambrian, Bohemia. A, earliest stage (protaspis), ×12. B, later stage, with three segments behind the head, ×12. C, with more distinct glabella furrows and four segments behind the head, ×12. D, with six segments behind the head, ×10.

E—H. *Phacops* (*Odontochile*) *socialis*, Ordovician, Bohemia. × about 8. E, earliest known stage, with eyes at the margin, and three segments behind the head. F, later stage, with more distinct furrows on the glabella, and four segments behind the head. G, with eyes moved inward, and narrow free cheeks; six segments behind the head. H, free cheeks relatively larger and eight segments behind the head.

glabella usually reaches the front margin of the head. In later stages the pygidium becomes more distinct and increases in size; and the thoracic segments are gradually introduced between the head and the pygidium (C, D). At the same time the eyes move backwards and inwards until they attain their adult position, and the free cheeks

increase in size (H). The glabella often becomes rounded in front and relatively shorter; its furrows become more distinct, indicating the existence of five cephalic segments. In some cases (C, D) the facial suture appears first at the lateral margin of the head-shield; in others (G) at the anterior margin. Beecher considers that the protaspis of Trilobites corresponds to one of the nauplius stages (the metanauplius) of recent Crustacea, but that view is not accepted by Kingsley.

The youngest stages of some of the Olenellids are of interest since segmentation is shown on the cheeks by means of grooves which extend outwards from the glabella; in these forms the eye-lobe appears first as an out-growth from the front segment of the glabella.

The possession of antennæ, the biramous character of the other appendages, and the presence of five cephalic segments, show that the Trilobites belong to the Crustacea. The great variability in the number of segments in the thorax and pygidium, the leaf-like character of the appendages on the posterior part of the body, the large hypostome, and the gnathobases on the thoracic appendages seem to indicate that the Trilobites are related to the Phyllopod group of the Branchiopoda (p. 332), and especially to *Apus* and *Branchipus*; other features in which the two groups agree have been furnished by the discovery of the median unpaired eye and the caudal fork in Trilobites. But the Trilobites differ from the Phyllopods in the trilobation of the body, in the occurrence of a facial suture, and in the posterior segments being fused together to form a pygidium. In the character of their appendages the Trilobites are more primitive than the Phyllopods or any other Crustacea, since all except the first pair are very similar in structure and show but little specialisation in different regions of the body, and all are deeply biramous.

Other primitive characters are seen in the indication of segmentation on the dorsal surface of the head, and in the presence of a pair of appendages on every segment of the body except the last. The Trilobites differ from other Crustacea in having only one pair of pre-oral appendages.

In the general form of the dorsal exoskeleton and in the position of the compound eyes some of the Trilobites show a resemblance to the Xiphosura (p. 361); this appears to be due to adaptation to a similar mode of life rather than to any close relationship, since the essential morphological features of the two groups are distinct. It is probable that most of the Trilobites lived on the sea-floor and were able to burrow in the sand or mud in the same way that *Limulus* does.

Agnostus. Body small, head-shield and pygidium similar in form and size; eyes and facial suture absent; glabella does not reach the anterior border of the head, and has a small lobe at each of the posterior angles. Thorax formed of 2 segments, axis wide, pleuræ grooved. Segmentation not shown on the lateral parts of the pygidium. *Olenellus* Beds to Bala Beds. Ex. *A. pisiformis*, Lingula Flags.

Microdiscus. Similar to *Agnostus* but with from 2 to 4 segments in the thorax, and axis of pygidium with numerous distinct segments. *Olenellus* Beds to Lingula Flags. Ex. *M. punctatus*, Lingula Flags.

Trinucleus. Head-shield large, with long genal spines, and a broad flat, ornamented border; glabella inflated, pyriform, furrows sometimes absent. Eyes generally absent. Facial suture absent or indistinct. Thorax with 6 segments, pleuræ grooved, straight, but slightly curved near their extremities. Pygidium short, triangular, margin entire. Arenig to Bala Beds. Ex. *T. concentricus*, Bala Beds.

Ampyx. Similar to *Trinucleus.* Head shield triangular, without a border, and with a long straight spine given off from the front of the glabella; facial sutures near the external margin, not continuous in front; free cheeks very narrow. Arenig to Wenlock Beds (chiefly Ordovician). Ex. *A. nudus*, Llandeilo Beds.

Olenellus. Head-shield large, semicircular, with a border and genal spines; glabella of nearly the same width throughout, the front lobe longer than the others; facial sutures not visible; eyes large, elongate, curved, joined to the front segment of the glabella. 14 segments in the thorax; pleuræ grooved and produced into backwardly-curved spines; the third segment larger than the others and with longer spines. Pygidium elongate, spine-like, without lateral lobes. Lower Cambrian. Ex. *O. thompsoni.*

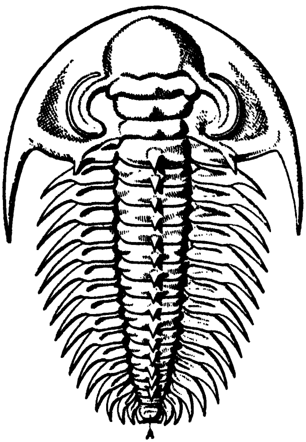


Fig. 146.

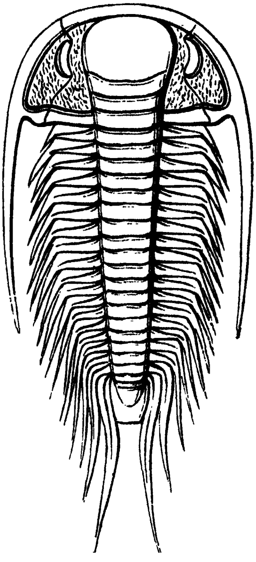


Fig. 147.

Fig. 146. *Holmia kjerulfi*, Lower Cambrian. (After Holm.) Natural size.

Fig. 147. *Paradoxides davidis*, from the Menevian Beds. × ½.

Mesonacis. Similar to *Olenellus.* Thorax elongated, tapering posteriorly, consisting of 15 anterior segments, behind which are 10 shorter segments with the pleuræ less well developed; the axis of the 15th segment bears a long backwardly-directed spine. Pygidium small, plate-like. Lower Cambrian. Ex. *N. vermontana.*

Holmia (fig. 146). Similar to *Olenellus*. A spine at the posterior margin of the head-shield between the glabella and the genal spine. Thorax of 16 segments, the third not enlarged; pleuræ produced into narrow, separated spines. A row of spines extends down the axis of the body from the neck-ring nearly to the pygidium. Pygidium small, plate-like, with indications of segments on the axis. Lower Cambrian. Ex. *H. kjerulfi*.

Callavia. Similar to *Holmia*. Glabella narrow, especially in front. Pleuræ produced into broad spines. A long spine from the neck-ring. Lower Cambrian. Ex. *C. bröggeri*.

Paradoxides (fig. 147). Body large, elongated, narrowed posteriorly. Head-shield broad, semicircular, with a border, and long genal spines; glabella broad in front, with 2 to 4 furrows on each side, some of which are continuous across. Facial sutures extend from the posterior to the anterior border. Eyes large and arched. Thorax long, of 16 to 20 segments; pleuræ grooved and produced into long backwardly-directed spines. Pygidium very small, plate-like, its axis with 2 to 8 segments. Middle Cambrian. Ex. *P. davidis*, Menevian; *P. bohemicus*, Cambrian.

Olenus (fig. 148). Body oval; head-shield larger than the pygidium, with a narrow border, and with genal spines; glabella not reaching the anterior border, and not expanding in front, usually with three pairs of furrows; facial sutures extend from the posterior margin (near the genal angle) to the front border; eyes a little in front of the middle of the cheeks, and united to the front of the glabella by an eye-line. Thorax of from 12 to 15 (typically 14) segments; axis narrow, pleuræ with short points. Pygidium small, with 3 or 4 segments indicated on the axis, and with entire border. Lingula Flags to Tremadoc Beds. Ex. *O. gibbosus*, *O. cataractes*, Lingula Flags. *Parabolina*, *Peltura*, *Parabolinella*, *Leptoplastus*, *Eurycare*, and *Sphærophthalmus* are closely related to *Olenus*.

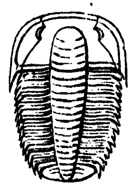


Fig. 148. *Olenus cataractes*, from the Lingula Flags. Natural size.

Conocoryphe (=*Conocephalites*). Head-shield semicircular, with a furrow inside the border, with genal spines (not always preserved); axial furrows deep, glabella narrow in front and with 3 or 4 backwardly-directed furrows and a well-marked neck-furrow; free cheeks narrow; eyes absent. Facial sutures begin just within the genal angles, and cut the front margin. Hypostome convex, formed of a central oval portion surrounded by a narrow border. Thorax with 14 or 15 segments; pleuræ grooved. Pygidium small, margin entire, axis with from 2 to 8 segments. Lower Cambrian to Tremadoc Beds. Ex. *C. lyelli*, *C. sulzeri*, Lower Cambrian.

Angelina. Body oval. Head-shield with long genal spines, glabella parabolic, without furrows; eyes small, near the middle of the cheeks. Thorax with 14 or 15 segments, pleuræ faceted. Pygidium short, margin provided with two teeth, axis of 4 or 5 segments. Tremadoc Beds. Ex. *A. sedgwicki.*

Calymene (fig. 139). Head-shield semicircular, genal angles rounded, occasionally pointed; glabella inflated, broadest behind, with three pairs of lateral furrows separating three globular lobes on each side. Eyes small, prominent. Facial sutures extending from the genal angles to the anterior border, where they are connected by a transverse suture below the margin. Thorax of 13 segments, axis prominent, pleuræ grooved and faceted. Pygidium with 6 to 11 segments, margin entire. Arenig to Upper Ludlow. Ex. *C. tuberculata*, Wenlock Limestone.

Homalonotus (fig. 149). Body large, elongated, with indistinct trilobation. Head-shield broad, genal angles rounded, furrows on the glabella indistinct or absent. Eyes small. Facial suture passing from the genal angles to the front margin, and often continuous in front. Thorax with 13 segments; axis wide, not well marked. Pygidium triangular, axis with 10 to 14 segments. Arenig to Devonian. Ex. *H. delphinocephalus*, Wenlock Beds; *H. bisulcatus*, Ordovician.

Ogygia. Body oval, nearly flat. Head-shield large, semicircular, with a flattened border; glabella distinct, wider in front, with 4 or 5 lateral furrows. Eyes large. Facial sutures pass from the posterior border to the front margin, and are generally continuous at the margin. Free cheeks large. Hypostome not notched. Thorax of 8 segments, axis narrow, distinct; pleuræ grooved, usually with

pointed ends. Pygidium large, semicircular, margin entire, axis of numerous segments. Tremadoc to Llandeilo Beds. Ex. *O. buchi*, Llandeilo Beds.

Asaphus (figs. 142, 150). Body oval, surface smooth or with striæ. Head-shield large, semicircular with a flattened border, genal

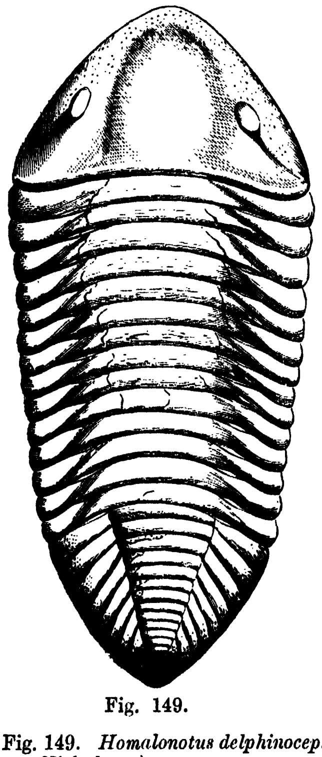


Fig. 149.

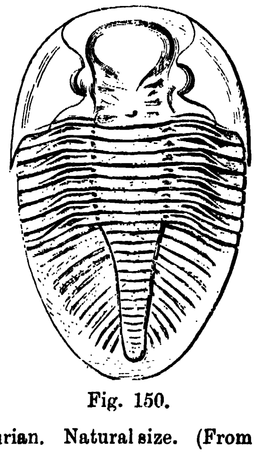


Fig. 150.

Fig. 149. *Homalonotus delphinocephalus*, Silurian. Natural size. (From Nicholson.)
Fig. 150. *Asaphus tyrannus*, from the Llandeilo Beds. × ½.

angles rounded or spinose; glabella indistinctly defined, wide in front, with indistinct lateral furrows. Eyes large. Facial sutures pass from the posterior to the anterior margin and are generally continuous at the front margin. Free cheeks large. Hypostome notched

posteriorly. Thorax formed of 8 segments, axis rather broad, pleuræ obliquely grooved, with rounded extremities. Pygidium of about the same size as the head, rounded, formed of numerous segments; margin entire. Tremadoc to Bala Beds. Ex. *A. tyrannus*, Landeilo. Sub-genus *Asaphellus*: hypostome not notched. Tremadoc Beds. Ex. *A. homfrayi.*

Illænus. Body oval, convex. Head-shield large, semicircular; glabella indistinctly limited except near the posterior end, without furrows externally. Eyes remote from one another. Facial sutures commence on the posterior border, cut the anterior border in front of the eye, and unite on the inferior surface. Free cheeks small. Thorax with usually 10 segments, axis broad, pleuræ neither grooved nor ridged. Pygidium large, semicircular, axis indistinct, segments not visible externally. Arenig to Wenlock. Ex. *I. davisi*, *I. bowmanni*, Bala Beds.

Æglina (fig. 140). Head-shield large; glabella large, convex, projecting beyond the margin in front. Cheeks narrow; eyes very large, occupying nearly all the free cheeks. Facial sutures discontinuous, close to the glabella. Thorax with 5 or 6 segments, axis broad, pleuræ grooved. Pygidium rounded, axis short. Arenig to Bala Beds. Ex. *Æ. binodosa*, Arenig Beds.

Bronteus. Head-shield large, semicircular, genal angles pointed. Glabella expanding rapidly in front, with 3 lateral furrows in some species, none in others. Facial sutures start from the posterior border and are discontinuous in front. Free cheeks large; eyes crescentic, placed near the posterior border. Thorax with 10 segments, pleuræ ridged. Pygidium very large, fan-shaped; axis very short; lateral lobes large, with radiating grooves. Bala Beds to Devonian. Ex. *B. flabellifer*, Devonian.

Harpes. Form similar to *Trinucleus*, but border of head-shield broader, finely punctate, and extended posteriorly to near the end of the thorax instead of bearing narrow genal spines. Glabella short, convex, not expanded in front. Eyes consist of 2 or 3 lenses, and are usually joined to the front part of glabella by an eye-line. Thorax with 22 to 29 segments; axis narrow, pleuræ long, grooved. Ordovician to Devonian. Ex. *H. ungula*, Ordovician.

Phacops. Head-shield nearly semicircular; glabella prominent, broadest in front, with 3 or 4 furrows, which are sometimes indistinct;

facial sutures commencing on the lateral borders of the cheeks in front of the genal angle, and continuous in front of the glabella. Eyes generally large, formed of large, distinct lenses. Thorax with 11 segments, pleuræ grooved. Pygidium variable. Ordovician to Devonian.

Phacops, as defined above, may be divided into:

Phacops (restricted): glabella inflated and expanded in front, with the two anterior furrows obscure. Eyes large. No genal spines. Silurian and Devonian. Ex. *P. stokesi*, Silurian.

Trimerocephalus: glabella furrows obscure or absent. Eyes small. No genal spines. Devonian. Ex. *T. lævis*.

Acaste: glabella not much expanded in front, all the furrows distinct. Ordovician and Silurian. Ex. *A. downingiæ*, Silurian.

Chasmops: glabella greatly expanded in front, two anterior furrows large, two posterior very small. With genal spines. Ordovician. Ex. *C. conophthalmus*, Bala Beds.

Odontochile (= *Dalmanites*)*:* glabella not much expanded, all the furrows distinct. Genal spines long. Pleuræ often produced into spines. Silurian and Devonian. Ex. *O. caudatus*, Silurian.

Cheirurus (fig. 151). Head-shield semicircular, genal angles pointed or with spines; glabella convex, oblong or ovoid, with three pairs of furrows which are sometimes continuous across, the last pair uniting with the neck-furrow. Facial sutures continuous in front and ending on the external margins. Free cheeks small; eyes prominent. Thorax with usually 11 segments, pleuræ grooved, and produced into spines. Pygidium small, with 4 segments, lateral lobes with backwardly-directed spines. Tremadoc to Devonian. Ex. *C. articulatus*, Devonian; *C. bimucronatus*, Bala to Ludlow Beds; *C. juvenis*, Bala Beds.

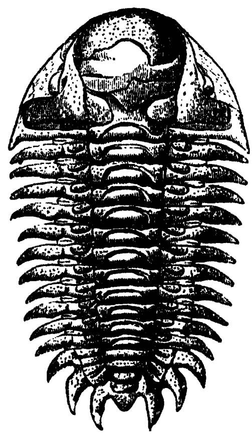


Fig. 151. *Cheirurus insignis*, Silurian. (From Nicholson after Barrande.) Natural size.

Deiphon. Glabella globular without furrows. Fixed cheeks forming two long curved spines. Thorax with 9 segments; pleuræ in the form

of free spines. Pygidium short, prolonged into two spines on each side. Llandovery and Wenlock. Ex. *D. forbesi.*

Sphærexochus. Glabella large, spheroidal, with 3 pairs of furrows—the two anterior indistinct, the posterior curving backwards and joining the deep neck-furrow. Cheeks small; eyes small, near the axial furrow; facial suture starts from the genal angle. Thorax with 10 segments; pleuræ without grooves, with rounded ends. Pygidium small, with 3 segments. Ordovician and Silurian. Ex. *S. mirus*, Wenlock Limestone.

Staurocephalus. Glabella with a spherical lobe projecting in front of the cheeks; the remainder of the glabella narrow and cylindrical with 2 pairs of furrows and a deep neck-furrow. Cheeks very convex, with a flat border. Facial suture starts from the lateral margin and cuts the front margin. Eyes on stalks. Thorax with 10 segments; pleuræ ridged, produced into spines. Pygidium small, of 4 segments, with pleuræ produced into spines. Bala to Wenlock Limestone. Ex. *S. murchisoni*, Wenlock Limestone.

Encrinurus. Head-shield covered with tubercles; with a flat border, and pointed genal angles; glabella pyriform, confluent with the border in front, its furrows indistinct or absent; eyes small, on short peduncles. Facial sutures continuous in front, ending just in front of the genal angles. Free cheeks narrow. Thorax with 11 similar segments, pleuræ ridged. Pygidium narrow, triangular, with many segments in the axis, with 6 to 12 pleuræ bent backwards and diverging from the axis. Bala to Upper Ludlow. Ex. *E. punctatus*, Wenlock Limestone.

Cybele. Similar to *Encrinurus*. Three pairs of more distinct glabella furrows; border continuous in front of the glabella; genal angles usually rounded; facial sutures continuous in front. Thorax with 12 segments; pleuræ of the first 5 with blunt ends, those of the remaining 7 produced into spines. Pygidium with 4 or 5 pleuræ which bend sharply backwards and converge towards the axis. Ordovician. Ex. *C. verrucosa*, Bala Beds.

Lichas. Test covered with tubercles. Head-shield convex, relatively small, with genal spines. Glabella broad, with a central raised part, furrows directed backwards. Facial sutures pass from the posterior to the anterior border. Cheeks and eyes small. Thorax

with 9 or 10 segments; pleuræ grooved, ending in rather long spines. Pygidium large, showing 2 or 3 segments, lateral parts produced into spines. Llandeilo to Wenlock. Ex. *L. anglicus*, Wenlock.

Acidaspis (fig. 152). Head-shield broad, its trilobation not well marked, with genal spines, and usually with spines at the margin of the head; glabella with a pair of longitudinal furrows parallel to the axial furrows, and with two or three lateral furrows. Facial sutures start from the posterior margin just within the genal angle and cut the front margin. Free cheeks large. Eyes connected with the glabella by an eye-line. Thorax with 9 or 10 segments, pleuræ with ridges produced into long spines. Pygidium small, with long spines. Llandeilo Beds to Devonian. Ex. *A. barrandei*, *A. brighti*, Wenlock.

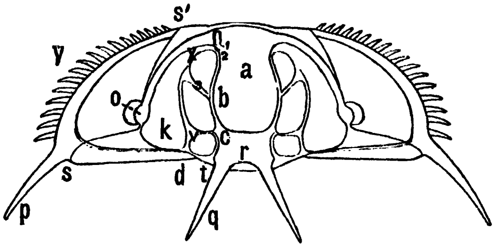


Fig. 152. *Acidaspis prevosti*, from the Silurian. Head-shield. (After Barrande.) 1, 2, 3, first, second, and third glabella furrows (the first usually indistinct); *a*, central part of the glabella; *c—b—n*, inner furrow of glabella; *c—v*, neck-furrow; *d—v—x*, axial furrow; *k—x*, fixed cheek; *o*, eye; *o—n*, eye-line; *p*, genal spines; *q*, spines from neck-ring; *r*, neck-ring; *s—s'*, facial suture; *y*, spines. Enlarged.

Phillipsia. Body oval; glabella with nearly parallel sides, with 3 or 4 narrow lateral furrows, of which the posterior one curves backwards and joins the deep neck-furrow, thus cutting off a basal lobe. Facial sutures cut the posterior border obliquely, and the anterior border in front of the eye. Free cheeks large; eyes large, reniform. Thorax with 9 segments, pleuræ grooved. Pygidium semicircular, with 12 to 18 segments, margin entire. Devonian to Permian. Ex. *P. derbiensis*, Carboniferous.

Proetus. Closely allied to *Phillipsia* but with fewer segments in the pygidium. Ordovician to Carboniferous, chiefly Devonian. Ex. *P. fletcheri*, Wenlock.

Griffithides. Body oval; glabella with inflated basal lobes cut off by the posterior furrow, and without other lateral furrows; main part of glabella pyriform; eyes rather small. Thorax with 9 segments. Pygidium rounded, with about 13 segments. Carboniferous Limestone. Ex. *G. seminiferus.*

Distribution of the Trilobita

The Trilobites are confined to the Palæozoic period, and form one of the most important and striking features in the faunas of the Lower Palæozoic deposits. They occur first in the Lower Cambrian Beds, and reach their maximum in the Ordovician. In the Silurian, Trilobites are still abundant, but become less important in the Devonian, and in the Carboniferous are represented by four genera only. In Europe they do not extend beyond the Carboniferous Limestone, but in North America one species of *Phillipsia* has been found in the Permian.

Already in the Cambrian period the Trilobites were represented by a considerable variety of forms, showing that even then the group must have been of considerable antiquity, but at present no traces of the ancestors of the Cambrian forms have been found. It is in the Cambrian System that we meet with the largest, as well as the smallest Trilobites, *e.g. Paradoxides* and *Agnostus.* As a whole, it may be said that the Trilobites which are confined to the Cambrian period are characterised by the possession of a large number of thoracic segments, and of a small pygidium (fig. 147); whereas, in the Ordovician, most of the characteristic genera have fewer segments in the thorax and possess large pygidia (fig. 150).

The most important genera found in the different systems are mentioned below; those marked with an asterisk * occur only in one system.

Cambrian. *Agnostus*, *Microdiscus**, *Paradoxides**, *Olenellus**, *Mesonacis**, *Holmia**, *Sao**, *Ellipsocephalus**, *Concoryphe**, *Olenus**, *Niobe*, *Angelina**.

Ordovician. *Agnostus*, *Ampyx*, *Trinucleus**, *Ogygia*, *Asaphus*, *Illænus*, *Æglina**, *Calymene*, *Cybele**, *Lichas*. *Ogygia*, *Asaphus*, *Trinucleus* and *Ampyx* are abundant.

Silurian. *Calymene*, *Homalonotus*, *Illænus*, *Phacops*, *Cheirurus*, *Deiphon**, *Sphærexochus*, *Encrinurus*, *Acidaspis*, *Proetus*, *Lichas*. *Calymene* and *Phacops* are particularly abundant.

Devonian. *Homalonotus*, *Bronteus*, *Phacops*, *Cheirurus*, *Proetus*.

Carboniferous. *Phillipsia*, *Griffithides**, *Brachymetopus**.

SUB-CLASS II. BRANCHIOPODA

The Branchiopoda include the water-fleas (*Daphnia*, etc.) and other forms. The body, except in one group, is distinctly segmented, and often the greater part, or sometimes the whole, is covered by a carapace which may be shield-like, as in *Apus*, or in the form of a bivalved shell resembling a lamellibranch, as in *Estheria* (fig. 153); in some forms there is no carapace. The number of segments in the trunk varies very widely, there being in some cases as many as 42; but no satisfactory differentiation of these segments into thorax and abdomen can be recognised.

On the head there are generally two pairs of antennæ one of mandibles, and one or two of maxillæ; the maxillæ are small and in some cases the second pair are absent. The trunk bears several pairs of swimming-feet which are generally uniform in structure; they are flattened and leaf-like, and their basal parts function as jaws (gnathobases). Some of the posterior segments of the trunk may be without appendages. The last segment of the body (the telson) generally bears a caudal fork, having the form of a pair of spine-like or plate-like processes or of jointed

filaments. A pair of compound eyes are usually present, and often also a simple unpaired median eye; the former are usually sessile, but in some cases are borne on movable stalks.

The Branchiopoda live mainly in fresh water, but some are found in the sea, in salt lakes, and in brackish water. Only a few genera are found fossil. The group is divided into four Orders, (1) the Anostraca, (2) the Notostraca, (3) the Conchostraca, (4) the Cladocera. The first three Orders are often grouped together as the Phyllopoda. The Cladocera are not definitely known as fossils.

Order 1. **Anostraca.** The body is elongate and consists of numerous segments. There is no carapace. The paired eyes are stalked. A form similar to the living *Branchipus* has been found in the Oligocene of the Isle of Wight. Other genera which appear to belong to this Order occur in the Middle Cambrian of British Columbia.

Order 2. **Notostraca.** Carapace in the form of a dorsal shield covering the anterior part of the body. Eyes sessile. Caudal fork consists of jointed filaments. The living form *Apus* has been recorded from the Trias. The earliest representative of the Order is *Protocaris*, which resembles *Apus* and is found in the Lower Cambrian of North America. A few other genera occur in the Middle Cambrian of British Columbia.

Order 3. **Conchostraca.** Carapace forming a bivalved shell covering the entire body. Eyes sessile.

The principal genus is **Estheria** (fig. 153) in which the valves are thin, horny; ovate, oblong or quadrilateral, united at the straight dorsal border; the surface is covered with concentric ridges or striæ. Old Red Sandstone, Coal Measures, Permian, Trias, Wealden, Recent. Lives in fresh or rarely in brackish water.

Fig. 153. *Estheria minuta*, from the Trias. ×3.

SUB-CLASS III. OSTRACODA

The Ostracods (fig. 154) are indistinctly segmented and generally of minute size. The body is usually compressed laterally, and is completely enclosed in a bivalved carapace, which may be horny or calcareous. One valve is placed on each side of the animal, and the two valves are joined together dorsally by an elastic ligament which serves to open the shell; sometimes a hinge is formed by means of interlocking teeth and ridges; an adductor muscle passes from the interior of one valve to the other and by its contraction the shell is closed; usually the muscular

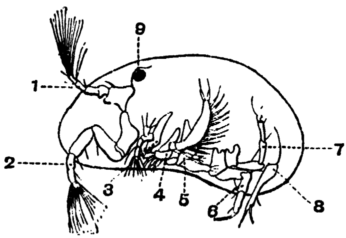


Fig. 154. Lateral view of *Cypris candida*. (After Zenker.) 1, antennules; 2, antennæ; 3, mandibles; 4, first maxillæ; 5, second maxillæ; 6, 7, first and second pairs of legs; 8, tail; 9, eye. Enlarged.

impression can be seen from the outside. There are seven pairs of appendages, which can be protruded when the shell is opened. In some of the marine forms the shell is notched anteriorly so as to allow the antennæ to pass through when the shell is closed. The head carries two pairs of large antennæ which are used for locomotion, one pair of mandibles, and two of maxillæ; the mandibles have a palp, usually large, which is not present in the Branchiopoda. The trunk has two or three pairs of appendages, which are not leaf-like; the posterior part is without appendages and

terminates in a caudal fork. A simple unpaired median eye is usually present and sometimes lateral compound eyes also. Respiration takes place by means of the general surface of the body. The carapace is in almost all cases the only part which occurs fossil; its surface may be smooth or variously ornamented.

Leperditia. Carapace thick, smooth, convex, elongated, a little higher posteriorly. The right valve larger than the left. Hinge-line straight; ventral margin rounded. There is a small tubercle (eye-spot) placed anteriorly near the hinge; and posterior to it is a slightly elevated circular area. Ordovician to Carboniferous. Ex. *L. hisingeri*, Silurian; *L. okeni*, Carboniferous.

Primitia. Carapace generally equivalve, convex, oblong or ovate. Hinge-line straight. Each valve has a transverse groove which starts from the hinge-line. Ordovician to Permian. Ex. *P. strangulata*, Bala Beds.

Beyrichia (fig. 155). Carapace elongated, inflated, posterior border a little higher than the anterior; dorsal border straight, ventral border semicircular. Two or three large furrows pass from the dorsal towards the ventral edge; the parts between the furrows are convex and often tuberculate, the middle part being the smallest. Ordovician to Carboniferous. Ex. *B. complicata*, Llandeilo and Bala.

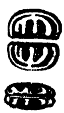


Fig. 155. *Beyrichia complicata*, Bala Beds. The lower figure shows the dorsal aspect of the united valves. × 2.

Entomis. Carapace equivalve, almond-shaped, with a deep transverse furrow which passes from the dorsal border (a little in front of the middle) towards the ventral border. Surface generally striated. Anterior margin notched for the passage of the antennæ. Ordovician to Carboniferous. Ex. *E. tuberosa*, Silurian.

Cythere. Shell oblong-ovate or subquadrate, highest in front; smooth or ornamented with pits, spines, or ridges. Hinge with teeth anteriorly and posteriorly. Permian to present day (chiefly Cretaceous and later). Ex. *C. striato-punctata*, Eocene; *C. punctata*, Pliocene.

Cypris (fig. 154). Carapace thin, smooth or punctate, kidney-shaped or oval; ventral edge often concave. Left valve the larger. Hinge without teeth. Tertiary to present day. Fresh water. Ex. *C. faba*, Miocene; *C. gibba*, Oligocene to present day.

Cypridea. Valves ovate-oblong, convex in the middle, broad at the anterior third, narrower behind; with a notch at the anterior ventral angle behind a beak-like process. Surface smooth, punctate, or tuberculate. Hinge-margin straight, along the middle third of the dorsal edge. Left valve the larger. Purbeck, Wealden, and Oligocene. Fresh water. Ex. *C. valdensis*, Wealden Beds, etc.

Distribution of the Ostracoda

The Ostracods have a very wide distribution at the present day; many forms are marine, and some are abundant in fresh water. The marine forms often occur in shoals; some are pelagic, but others live on the sea-floor and are more abundant in shallow than in deep water, only fifty-two species being found beyond the 500 fathom line.

The fossil forms are very numerous, the earliest occurring in the Upper Cambrian. *Leperditia*, *Primitia*, and *Beyrichia* are abundant in the Ordovician and Silurian; *Entomis* in the Devonian; and *Cypridina and Bairdia* in the Carboniferous. *Cypridea* is common in the Purbeck and Wealden Beds; and *Cythere* in the Tertiary formations.

SUB-CLASS V. CIRRIPEDIA

The Cirripedes include the barnacles, acorn-shells, etc. —forms which differ considerably in appearance from the other crustaceans and were for a long time regarded as molluscs. The body is completely enclosed in a "mantle" formed by a fold of the skin, which commonly secretes a calcareous shell. The animal, in the adult state, is fixed

to a foreign object by the anterior end of the head, either directly or by means of a muscular peduncle. The segmentation of the body is indistinct. The head bears one or two pairs of antennæ (the second pair usually absent in the adult), one pair of mandibles, and two pairs of maxillæ. The trunk has usually six pairs of biramous feathery limbs (or "cirri"). The posterior part of the trunk (abdomen) is much reduced and without appendages. Heart and vascular system are absent; nearly all forms are hermaphrodite. The shell consists of several pieces, the number and arrangement of which are of great systematic importance; in *Lepas* (which possesses a peduncle) there are five, two are placed on each side of the body, those near the peduncle being termed the *scuta* (fig. 156, *a*), those at the upper end the *terga* (*b*), and there is also one unpaired part placed dorsally, the *carina* (*c*). In some genera the peduncle is covered by rows of scale-like plates. *Balanus* has no stalk; its shell consists of a tube or truncated cone formed of six pieces, at the top of which the scuta and terga are placed and form an operculum. In Cirripedes in which a peduncle is present the remainder of the body is known as the *capitulum*.

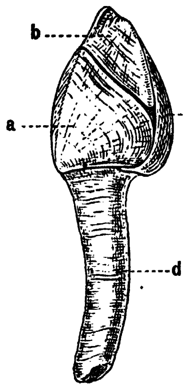


Fig. 156. *Lepas australis*, Recent. *a*, scutum; *b*, tergum; *c*, carina; *d*, peduncle. Natural size. (After Darwin.)

Distribution of the Cirripedia

The Cirripedes are all marine, and the greater number are found in shallow water, particularly near the coasts, *Balanus* being especially characteristic of littoral regions. At depths greater than 1000 fathoms, only two genera, *Scalpellum* and *Verrucosa*, have been found, and these are not confined to deep water.

Cirripedes are rare in the Palæozoic and early Mesozoic formations, but become moderately common in the Chalk, and are abundant in some of the later Tertiary deposits. The earliest undoubted representative of the group is *Hercolepas* from the Upper Silurian of Gothland; *Protobalanus* and *Palæocreusia* are found in the Middle Devonian of New York; all of these are sessile forms (*i.e.* without a peduncle). The Palæozoic genera *Turrilepas*, *Plumulites* and *Lepidocoleus* have usually been regarded as Cirripedes, but their systematic position is still uncertain. *Pollicipes* ranges from the Upper Jurassic, and *Scalpellum* from the Cretaceous to the present day. *Verruca, Loricula, Brachylepas* and *Pycnolepas* are found in the Chalk. *Proverruca*, from the Chalk, is of interest since it forms a link between the stalked Pollicipedidæ and the sessile Verrucidæ. *Balanus* appears in the Eocene, and *Lepas* in the Pliocene.

SUB-CLASS VI. MALACOSTRACA

The Malacostraca are usually of larger size than the Crustacea belonging to the four preceding groups. With the exception of the Leptostraca, the number of segments is constant, there being eight in the thorax, and six in the abdomen (not including the telson), making altogether nineteen segments in the body. The abdomen is clearly

marked off from the thorax by the character of the appendages. In some cases the development is direct, the young having the same or nearly the same form as the parent, but usually larval stages occur; the principal larval form is the zoæa, but a nauplius stage may also occur.

In many groups of the Malacostraca a dorsal shield or carapace is present, and usually coalesces with the terga of some or all of the thoracic segments, forming a *cephalo-thoracic shield* or *carapace* (fig. 162, *a*—*c*). The telson (*e*)—a median plate at the end of the abdomen—does not terminate in a caudal fork except in the Leptostraca. Each segment of the body, except the telson, usually carries a pair of appendages. The first pair of antennæ (unlike those in the preceding groups) are biramous. In some of the Malacostraca the thoracic appendages are all biramous; but often, with the exception of some of the anterior appendages, they are uniramous, the exopodites being absent. One or more (often three) of the anterior appendages of the thorax are modified so as to function as jaws, and are known as *maxillipedes*; the remainder of the thoracic appendages are used in locomotion. The appendages of the abdomen are biramous; the first five pairs are swimming legs (*pleopods*); the last pair (the *uropods*, fig. 162, *f*) are flattened and commonly form with the telson a fan-like tail-fin. In the Malacostraca the position of the genital apertures is constant (p. 308). A pair of compound eyes are usually present. Calcareous ossicles are developed in the stomach forming a 'gastric mill.'

There are five Orders of the Malacostraca:—(1) Leptostraca, (2) Syncarida, (3) Peracarida, (4) Eucarida, (5) Hoplocarida.

ORDER I. LEPTOSTRACA (PHYLLOCARIDA)

The Leptostraca differ in several respects from all the other Orders of the Malacostraca, and possess characters which connect them with the Branchiopods. Only four genera are now living, of which the commonest is *Nebalia*; they are small shrimp-like Crustacea, with the body later-

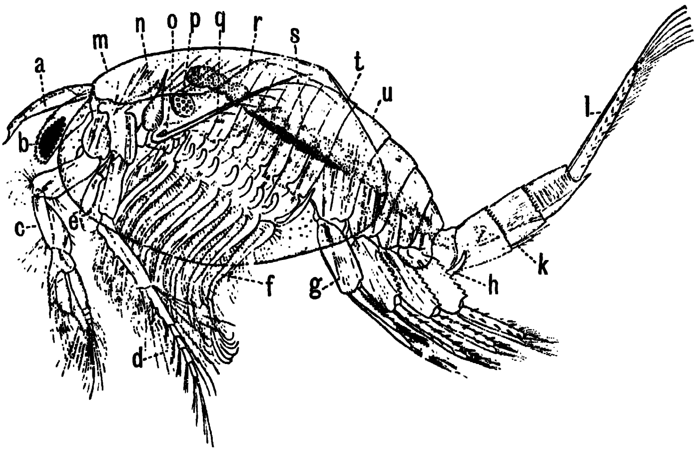


Fig. 157. *Paranebalia longipes*, Recent. (After Sars.) × 13. *a*, rostrum; *b*, eye; *c*, antennule; *d*, antenna; *e*, mandibular palp; *f*, last thoracic leg; *g*, first abdominal leg; *h*, *k*, rudimentary limbs of fifth and sixth abdominal segments; *l*, one half of the caudal fork; *m*, cephalic part of carapace; *n*, mandible; *o*, second maxilla; *p*, adductor muscle of carapace; *q*, first maxilla; *r*, first segment of thorax; *s*, ovary; *t*, last segment of thorax; *u*, first abdominal segment.

ally compressed. A large bivalved carapace (fig. 157, *m*) covers the head, the thorax, and some of the abdominal segments, but is united to the head only; the two valves are connected by an adductor muscle (*p*) just as is the case in the Ostracods and many Branchiopods. In front of

the carapace is a movable plate or *rostrum* (*a*). There are twenty segments in the body—five in the head, eight in the thorax (*r*—*t*), seven in the abdomen (*u*—*l*), and a telson carrying two pointed processes—the caudal fork (*l*). There are nineteen pairs of appendages, as in the Malacostraca; the head bears two pairs of antennæ (*c*, *d*), one pair of mandibles (*n*), two of maxillæ (*q*, *o*); on the thorax there are eight similar pairs of limbs (*f*) which are leaf-like and resemble those of Branchiopods; the abdomen has six pairs of appendages, the first four being large biramous swimming legs (*g*), the last two small and uniramous (*h*, *k*). The last abdominal segment is without appendages. The eyes are compound and stalked. The mandible bears a long, three-jointed palp (*e*). The anus opens on the telson between the two branches of the caudal fork.

The Leptostraca agree with the Malacostraca in having the abdomen and its appendages clearly marked off from the thorax; in the position of the genital apertures; in possessing eight segments in the thorax; in having nineteen pairs of appendages; and in the occurrence of a masticatory stomach. They differ from the Malacostraca in the bivalved carapace with an adductor muscle; in the possession of leaf-like thoracic legs, of seven abdominal segments, and a caudal fork. From most of the Malacostraca they are further distinguished by the presence of a movable rostrum, and by all the segments of the thorax being free. The group of the Malacostraca to which the Leptostraca seem to be most nearly allied is the Mysidæ—a family of the Mysidacea.

In the characters of the carapace and of the thoracic legs, and in the presence of a caudal fork, the Leptostraca resemble the Branchiopoda. But they differ from

them in the clear separation of the thorax from the abdomen; in the possession of a rostrum and a mandibular palp; and in the long anterior antennæ. Stalked eyes are found in some Branchiopoda and in many Malacostraca.

The Leptostraca are clearly generalised types, and are probably to be regarded as the last survivors of a primitive group of Crustacea. No representatives of the Order have, however, been yet discovered in post-Triassic rocks; but a number of Crustacea which closely resemble the living Leptostraca in the form of the body, with in some cases a movable rostrum, are found in the Palæozoic formations; they differ, however, in being much larger, and, usually, in the caudal fork consisting of more than two spine-like processes. Except in the genus *Hymenocaris* the appendages of these Palæozoic forms are almost unknown, and consequently it is difficult to determine their affinities satisfactorily. Masticatory organs in the stomach are stated to occur in some of the fossil forms. Some of the principal Palæozoic genera are described below.

Hymenocaris (fig. 158). Carapace semi-oval, smooth, not bivalved. Eight trunk-segments exposed, with four to six caudal spines. Lingula Flags. Ex. *H. vermicauda*.

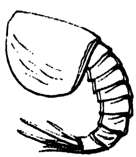


Fig. 158. *Hymenocaris vermicauda*, Lingula Flags. × ½.

Ceratiocaris. Carapace bivalved, often marked with striæ, suboval, narrow in front, truncated behind and with a lanceolate rostrum in front. Thorax and abdomen formed of fourteen or more segments, the first seven or more being covered by the carapace; telson long and pointed, with two lateral spines. Tremadoc Beds to Upper Silurian. Ex. *C. stygia*, *C. papilio*, Ludlow Beds.

Caryocaris (fig. 159). Carapace bivalved, pod-like, narrow smooth, rounded at one end, truncated at the other. Arenig Rocks. Ex. *C. wrighti.*

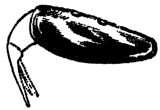


Fig. 159. *Caryocaris wrighti*, Arenig Rocks. Natural size. The abdomen has *not been found* attached to the carapace as shown above; some authors consider that the broad end of the carapace is anterior.

Dithyrocaris. Carapace large, bivalved, with a narrow anterior notch, rostrum unknown. Each valve semi-oval, truncated behind, with a median longitudinal ridge; another ridge at the dorsal margin where the valves join. Surface often with pits or granules. Exposed part of abdomen short, with a narrow, sharply-pointed telson bearing on each side a spine-like appendage. Devonian and Carboniferous. Ex. *D. colei*, Carboniferous.

Discinocaris. Carapace sub-circular, slightly convex, formed of one piece with a notch in front in which the triangular rostrum is placed. Surface with concentric linear ridges. Silurian. Ex. *D. browniana*, Llandovery.

Aptychopsis. Similar to the last, but carapace divided into two parts by a median suture which starts from the rostral notch. Silurian. Ex. *A. lapworthi*, Llandovery.

Distribution of the Leptostraca

The Leptostraca are all marine, and live mainly in shallow water or at moderate depths. In Britain the earliest representative is *Hymenocaris*, found in the Lingula Flags; *Ceratiocaris* appears in the Tremadoc Beds, but is most abundant in the Silurian. *Caryocaris* is characteristic of the Arenig Rocks. *Aptychopsis* and *Discinocaris* occur in the Silurian. *Echinocaris* is found in the Devonian; and *Dithyrocaris* in the Carboniferous. One genus, *Aspidocaris* (similar to *Discinocaris*), has been recorded from the Trias.

ORDER II. SYNCARIDA

The Syncarida are a small group of primitive Malacostraca, the living representatives of which are found in fresh water in Tasmania and Victoria, and belong to three genera of which the best known is *Anaspides* (fig. 160). The body is elongated and without a carapace, and is remarkable for the fact that all the thoracic segments are distinct, but the first is fused with the head. All the thoracic legs are similar in general character, and all, except the last one or two, are biramous; their coxopodites

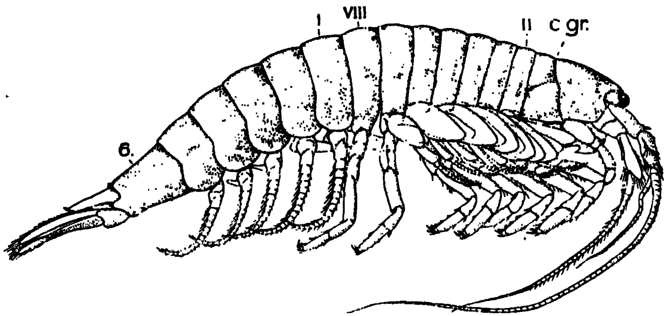


Fig. 160. *Anaspides tasmaniæ*, Recent. Tasmania. *c.gr*, 'cervical groove'; II, VIII, second and eighth thoracic somites; 1, 6, first and sixth abdominal somites. × 3. (From Woodward, 1908.)

bear externally two rows of plate-like gills, but these have not been found in fossil specimens. The abdomen is large, and the first five pairs of appendages consist of long, many-jointed exopodites and small endopodites; the appendages of the sixth segment form with the telson a tail-fin.

Fossil representatives of the Syncarida, closely resembling the living-forms, are found in the Carboniferous and Permian deposits; the genera *Palæocaris* (= *Præanaspides*) and *Acanthotelson* occur in the former, and *Uronectes*

(= *Gampsonyx*) in the latter. The principal feature in which *Palæocaris* differs from the living *Anaspides* is in the short, wedge-shaped first thoracic segment which is bounded in front by a groove.

ORDER III. PERACARIDA

The Peracarida are Crustacea in which a carapace may or may not be present, but when present it leaves not less than four of the thoracic segments free. The first thoracic segment is always fused with the head. The eyes may be either stalked or sessile. In the female a brood-pouch, for the protection of the eggs and the young, is formed by overlapping plates known as oostegites which are attached to the basal part (coxopodite) of some or all of the thoracic limbs. The Peracarida are divided into (1) Mysidacea, (2) Cumacea, (3) Tanaidacea, (4) Isopoda, (5) Amphipoda. Of these sub-orders the Cumacea and Tanaidacea are not known as fossils.

SUB-ORDER I. MYSIDACEA

A carapace is present and covers the greater part of the thorax, but does not coalesce dorsally with more than three of the thoracic segments, so that at least five segments remain free. The eyes, when present, are stalked. The thoracic limbs, except sometimes the first and second pairs, are biramous, the exopodites being used in swimming; the first and second pairs of these limbs are modified as maxillipedes. A tail-fin is formed by the lamellar appendages of the last abdominal segment.

Living Mysidacea, with a few exceptions, are marine, and many of them are pelagic. The fossil forms which have been referred to this group are found mainly in the

Carboniferous rocks, especially in the south of Scotland where they are sometimes numerous; the principal genera are *Pygocephalus, Anthrapalæmon, Pseudogalathea, Crangopsis,* and *Tealliocaris.* *Schimperella,* from the Trias, probably belongs to the Mysidacea, but no representatives of the group have yet been found in later deposits. The only fossil form in which the brood-pouch has been discovered is *Pygocephalus.* In the Upper Devonian *Palæopalæmon* is found, and may belong to this group.

SUB-ORDER IV. ISOPODA

In the Isopods (fig. 161) the body is usually flattened dorso-ventrally. There is no carapace, but the first thoracic segment (occasionally also the second) is fused with the head. The eyes are sessile. The thoracic appendages are without exopodites; the first pair are maxillipedes, the other seven are walking legs and are sometimes similar in size and form —hence the name Isopoda. The abdomen is often short, and usually some or all of its segments are fused together and with the telson. Some of the abdominal appendages function as gills.

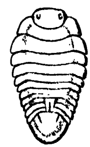


Fig. 161. *Archæoniscus brodiei,* from the Purbeck Beds. Slightly reduced.

Many Isopods are marine, but some are found in fresh water, whilst a few live on land (*e.g.* the wood-louse, *Oniscus asellus*). Many forms are parasitic, and infest fish and Crustacea.

Fossil Isopods are rare. Some Palæozoic forms (such as *Oxyuropoda* and *Præarcturus* from the Old Red Sandstone) have been referred to this group, but their systematic position is doubtful. Undoubted examples of this

Order are found in Jurassic and later formations: *Cyclosphæroma* in the Great Oolite and Purbeckian; *Urda* from the Solenhofen Limestone; *Archæoniscus* (fig. 161) in the Purbeckian; *Palæga* in the Middle Jurassic, the Cambridge Greensand, the Lower Chalk, and foreign Tertiary; and *Eosphæroma* in the Oligocene of the Isle of Wight.

SUB-ORDER V. AMPHIPODA

The Amphipoda (*e.g. Gammarus, Talitrus*) are usually of small size, and generally the body is compressed from side to side. Just as in the Isopods, there is no carapace, and the first thoracic segment (sometimes also the second) fuses with the head. The thoracic appendages have no exopodites; the first pair are maxillipedes; the appendages of the seven free segments bear the gills, and are divisible into an anterior group of four in which the terminal parts of the legs are directed backwards, and a posterior group of three in which the terminal parts are directed forward. The abdomen is usually elongated and carries six pairs of appendages; the three anterior serve for swimming, the three posterior for jumping. The eyes are sessile.

Some of the Amphipods are marine, others live in fresh water. The marine forms have a wide distribution, and are very numerous, especially in shallow water, and in Arctic and Antarctic seas.

Fossil Amphipods are very rare. A few Arthropods from Palæozoic formations have been referred to this group, but their systematic position is uncertain. Undoubted Amphipods are found in the Tertiary formations and belong mainly to genera which are still existing (*e.g. Gammarus* from the Miocene).

ORDER IV. EUCARIDA

The carapace fuses dorsally with all the thoracic segments. The eyes are stalked. There is no brood-pouch. The Eucarida are divided into two sub-orders (1) the Euphausiacea, (2) the Decapoda. The first is not known fossil.

SUB-ORDER II. DECAPODA

The Decapoda include lobsters (fig. 162), cray-fishes, crabs, etc. The carapace (*a*—*c*) is large and well developed, and covers all the segments of the thorax (*b*—*c*); frequently

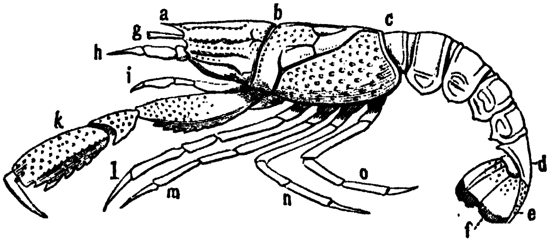


Fig. 162. *Glyphea regleyana*, Oxfordian. *a*, rostrum; *a*—*c*, cephalothorax; *b*, cervical sulcus; *c*—*e*, abdomen; *d*, sixth abdominal segment; *e*, telson; *f*, appendage (uropod) of sixth abdominal segment; *g*, eye; *h*—*o*, appendages of cephalothorax; *k*—*o*, ambulatory limbs. $\times \frac{2}{3}$.

it is marked out into an anterior and a posterior portion by a transverse groove,—the *cervical sulcus* (*b*). The carapace is often produced in front into a rostrum (*a*). The gills are connected with the bases of the thoracic appendages and to the lateral walls of the thoracic segments, and are placed in a chamber on each side of the thorax formed by the downward prolongation of the carapace. The appendages on the head are (1) antennules, (2) antennæ, (3) mandibles, (4, 5) maxillæ; the last three

pairs serve as jaws. On the thorax the first three pairs of limbs are modified as maxillipedes; the posterior five pairs (*k*—*o*) are the ambulatory limbs, which, in most cases, are uniramous owing to the absence of the exopodite; they consist of seven joints, and, commonly, some of them terminate in pincers or *chelæ*. The name 'Decapoda' is taken from these five pairs of ambulatory legs. The abdomen bears six, or fewer, pairs of appendages; the last pair (*f*) are often flattened and form with the telson (*e*) a tail fin. The eyes are compound and stalked. Most of the Decapod Crustacea are marine, the larger number living in shallow water; but some groups are found in fresh water, and others (some of the Anomura and Brachyura) have become terrestial in habit. The earliest undoubted representations of the Decapoda are formed in the Trias.

The Decapoda may be divided into two sections:—(1) the Natantia, (2) the Reptantia.

Section 1. *Natantia*

The body is usually compressed laterally, and a rostrum, which is usually compressed and serrated, is present. The thoracic legs are slender, but one of the first three pairs may be enlarged, and exopodites are sometimes present. The first segment of the abdomen is not much smaller than the others; the abdominal appendages are well-developed and used for swimming.

The Natantia are found first in the Trias, and become more abundant in the Jurassic; a few forms have been found in later deposits. Some of the Jurassic representatives of the group agree closely with the recent genus *Penæus*. *Æger* appears to be a primitive type of the group to which the living form *Stenopus* belongs.

Æger. Body laterally compressed. Abdomen long. Rostrum long, with small tubercles. Antennules nearly as stout, but not so long as the antennæ. Last maxillipedes long. First three pairs of legs with chelæ, the third pair longer than the others; the fourth and fifth pairs slender and flattened, without chelæ. Trias and Jurassic. Ex. *Æ. tipularius*, Solenhofen Limestone (Upper Jurassic).

Section 2. *Reptantia.*

The body is generally depressed; the rostrum is often absent, but when present is small and depressed. The thoracic legs are stout and without exopodites; the first pair are usually much larger than the others. The first segment of the abdomen is smaller than the others, and the first five abdominal legs are small and not used for swimming. This section appears first in the Trias, and is divided into four groups, (1) the Palinura, (2) the Astacura, (3) the Anomura, (4) the Brachyura.

1. *Palinura.*

The carapace is fused at the sides with the epistome (the region between the front of the mouth and the anterior margin of the carapace). The abdomen is large, well-plated, with well-developed pleura and a broad tail-fin (macrurous). The exopodites of the last pair of abdominal appendages are not usually divided by a distinct suture.

Eryon, found mainly in the Jurassic, lived in shallow water and possessed eyes; whereas the living forms (*Polycheles*, etc.) allied to it are blind and are found in deep water. Another group is represented by *Glyphea* and its allies, in which the thoracic legs are either not chelate or only imperfectly chelate; of this group *Pemphix* is found in the Trias; *Glyphea, Pseudoglyphea* and *Mecochirus* in the Jurassic; *Meyeria* and *Glyphea* in the Cretaceous.

Eryon (fig. 163). Cephalothorax flattened, usually broader than long, with a median dorsal ridge on the posterior part; the lateral margins usually dentate, and at the anterior third are two deep notches. Cervical sulcus sometimes absent. Rostrum short. The

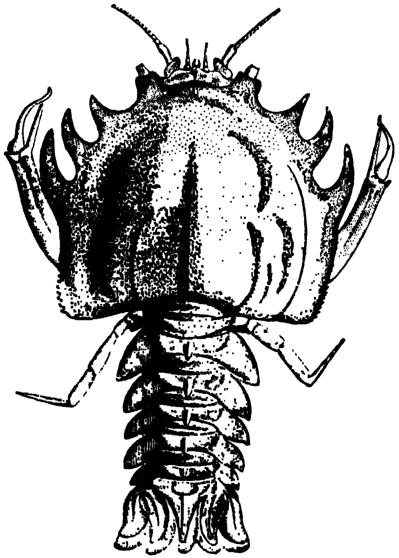


Fig. 163. *Eryon arctiformis*, Solenhofen Limestone (Upper Jurassic). (From Nicholson.) Natural size.

first four pairs of legs bear chelæ, the anterior pair being larger than the others. Abdomen of about the same length as the cephalothorax; the first segment very short. Telson trigonal. Trias to Lower Cretaceous. Ex. *E. propinquus*, Solenhofen Limestone.

Glyphea (fig. 162). Cephalothorax ornamented with granules, with a median dorsal suture; rostrum short. In front of the deep cervical sulcus are several spiny or tuberculate parallel ridges which extend towards the anterior margin. Posterior to the cervical sulcus are two oblique grooves which meet on the dorsal surface and bound a triangular lobe. The anterior pair of legs are much longer than the others; all are without chelæ. Abdomen long. Trias to Cretaceous. Ex. *G. regleyana*, Oxfordian; *G. rostrata*, Corallian.

Mecochirus (fig. 164). Carapace thin; rostrum short. Cervical sulcus deep, extending obliquely forward from the dorsal line. Antennæ as long or longer than the entire body. Legs not chelate; the first pair greatly elongated. Jurassic. Ex. *M. longimanus*, Solenhofen Limestone.

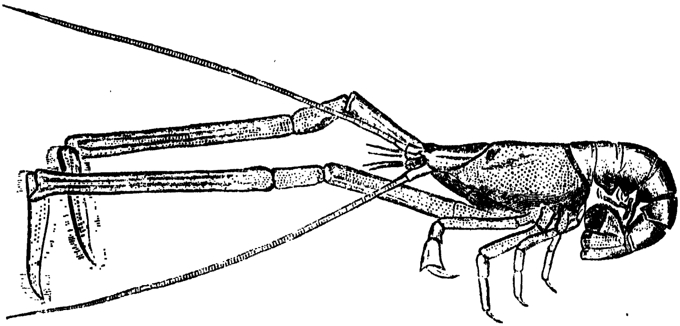


Fig. 164. *Mecochirus longimanus*, Solenhofen Limestone (Upper Jurassic). (From Nicholson, after Oppel.) × ½.

Meyeria. Cephalothorax laterally compressed, with a sharp rostrum, and a deep V-shaped cervical sulcus; with sharp, serrate, longitudinal ridges on the dorsal surface; the sides of the carapace covered with sharp granules. Behind the cervical sulcus is a faintly-marked oblique furrow on the sides of the carapace. Ambulatory legs slender. Abdomen semi-cylindrical, longer than the cephalothorax, and ornamented with rows of granules. Lower Cretaceous. Ex. *M. ornata*, *M. magna*.

2. *Astacura*

This includes the true lobsters and crayfishes. The carapace is not fused with the epistome. The abdomen is macrurous as in the Palinura. The exopodites of the last abdominal appendages are divided by a suture. The first three pairs of thoracic legs are chelate, the first pair being much enlarged.

The Astacura appear first in the Trias (*Clytiopsis*). The principal Jurassic form is *Eryma*. *Enoploclytia* and *Hoploparia* occur in the Cretaceous; the latter, which closely resembles the living lobster (*Homarus*), is also found in the Eocene.

Eryma. Body cylindrical. Cephalothorax covered with granules, with a median dorsal suture, a deep cervical sulcus, and a pointed rostrum. Behind the cervical sulcus are two nearly parallel grooves which unite at the sides. The three anterior pairs of legs with chelæ, the first pair being very large, the others small. Telson undivided. Lias to Upper Jurassic. Ex. *E. leptodactylina*, Solenhofen Limestone; *E. elegans*, Great Oolite, etc.

Enoploclytia. Body large, long, narrow; surface roughened with granules and tubercles. Cephalothorax elevated, narrowing in front, with a long dentate rostrum. Behind the deep cervical sulcus are one or two nearly parallel furrows, from which lateral branches pass to the cervical sulcus. First pair of legs very strong, with large chelæ having teeth on the inside of the fixed part; second and third pairs of legs slender, also with chelæ. Telson large, subtrigonal. Upper Cretaceous. Ex. *E. leachi*, Chalk.

Hoploparia. Body elongate, slightly compressed laterally. Carapace covered with fine granules. Rostrum very narrow, long, sharp and not dentate. Cervical sulcus deep, not reaching the margins of the carapace; in front of the cervical sulcus is a λ-shaped groove. The two anterior pairs of legs very long, provided with large chelæ. Abdomen sub-cylindrical. Lower Cretaceous to Eocene. Ex. *H. longimana*, Lower Greensand.

3. *Anomura*

The abdomen is generally soft or bent upon itself; its pleura are small or absent, and the tail-fin is often reduced. This group includes, amongst other forms, the hermit-crabs; it has but few fossil representatives, the principal genus being *Callianassa* which ranges from the Upper Jurassic to the present day.

4. *Brachyura*

This group includes the crabs. The abdomen is short and small; it is bent up underneath the thorax, and bears from one to four pairs of appendages, but is without a tail fin. The cephalothorax is broad. The carapace is fused with the epistome at the sides and usually also in front. The first thoracic legs are always chelate.

The first undoubted examples of the Brachyura are found in the Jurassic rocks, but only two or three genera are represented, of which *Prosopon* appears first in the Inferior Oolite and survives until the Lower Cretaceous, whilst *Protocarcinus* (= *Palæinachus*) is found only in the Forest Marble; these early forms are allied to the most primitive group of living crabs (the Homolodromiidæ), and also show characters which connect them with the lobsters (Astacura). In the Cretaceous the Brachyura become more abundant and are represented by *Palæocorystes*, *Eucorystes*, *Necrocarcinus* and several other genera. In the Eocene numerous forms occur, *Xanthopsis* and *Dromia* being common. The Brachyura attain their maximum at the present day.

Dromia. Carapace oval or rounded, very convex, with the entire surface punctate; anterior part with pointed elevations, posterior third with irregular ridges; divided into regions by two transverse grooves. Rostrum short, triangular. Orbital notches (in which the eyes rest) are very deep. First pair of legs strong, with large chelæ; second and third pairs short; fourth and fifth slender. Abdomen of six segments and a telson in both sexes. Eocene to present day. Ex. *D. lamarcki*, London Clay.

Palæocorystes. Carapace much longer than broad, tapering posteriorly, anterior border not dentate; rostrum short. Orbital notches large with two small fissures. Cervical sulcus well defined. The five anterior segments of the abdomen short, the sixth quadrangular. Gault and Eocene. Ex. *P. stokesi*, Gault.

Eucorystes. Carapace trapezoidal; anterior part with tortuous, band-like elevations; posterior part smooth or finely granular. Cambridge Greensand. Ex. *E. carteri.*

Necrocarcinus. Carapace rounded, separated into regions by distinct grooves, ornamented with a few prominent tubercles. Rostrum triangular. Orbital notches rounded, open above, with two small fissures. Gault to Chalk. Ex. *N. bechei*, Cambridge Greensand.

Xanthopsis. Carapace rounded, convex, surface punctate, the posterior portion with rounded elevations; the frontal border with four, and the anterior laterals with one to three, tooth-like processes. Orbital notches deep, without fissures. Chelæ unequal. Abdomen of the male narrow and formed of four segments and a telson. Abdomen of female broad, composed of six segments and a telson. Eocene. Ex. *X. leachi*, London Clay.

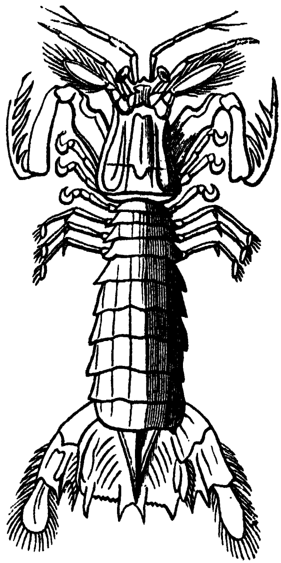


Fig. 165. *Squilla mantis*, Recent. (From Nicholson.) × ½.

ORDER V. HOPLOCARIDA

This includes one sub-order only.

SUB-ORDER. STOMATOPODA

In the Stomatopods (fig. 165) the body is long, and flattened dorso-ventrally; the carapace is short and does not cover the four posterior thoracic segments. At the front of the head there are two, small, movable segments which are not covered by the carapace; the first bears the stalked eyes, the second bears the antennules. A

rostral plate is articulated to the front of the cephalo-thoracic shield. The five anterior pairs of thoracic appendages have no exopodites and are directed forwards as maxillipedes; the three posterior pairs are slender biramous legs and are directed downwards. The abdomen is much larger than the anterior portion of the body; its five anterior appendages bear gills, and the sixth pair form with the broad telson a strong tail fin.

Squilla (fig. 165) is the best known genus of this sub-order. All the forms are marine and live in shallow water. The Stomatopods are very rare as fossils. A few Crustacea found in the Carboniferous have been referred to this group; but no undoubted representatives are known of earlier date than the Upper Jurassic. The genus *Sculda* occurs in the Solenhofen Limestone, and *Squilla* has been found in the Chalk of Lebanon and in some of the Eocene formations (London Clay, etc.).

CLASS III. MYRIAPODA

The Myriapoda include the millipedes, centipedes, and allied forms. The body consists of a distinctly-marked head, followed by segments which are usually numerous and similar in form, so that, externally, the limits of the thorax and abdomen cannot be defined. The head bears one pair of antennæ; and also mandibles and maxillæ. The segments behind the head (except the last) bear in some cases one, in others two, pairs of legs each; in the latter the segments are really double. The Myriapods breathe by means of tracheæ. Fossil representatives of this class are rare.

The two principal Orders are:—(1) the *Diplopoda*, or

millipedes, in which the body is usually more or less cylindrical, and each double segment bears two pairs of legs. Representatives of some of the living families occur in the amber found in the Oligocene Beds of Prussia and in other Tertiary deposits, *Julus* being found as far back as the Eocene.

The Palæozoic genera differ from the later representatives of the group and are regarded as constituting two extinct groups which are confined to the Palæozoic formations. The earliest examples are found in the Upper Silurian of Lanarkshire and belong to the genus *Archidesmus.* In the Old Red Sandstone of Scotland *Kampecaris* and *Archidesmus* occur. A larger number of forms (*Xylobius, Euphoberia, Anthracodesmus*) are found in the Carboniferous and Permian rocks.

(2) The *Chilopoda* or centipedes. The body is flattened dorso-ventrally, and each segment bears a single pair of legs. The earliest forms occur in the Coal Measures, and modern families are represented in the Oligocene amber and in some other Tertiary deposits.

CLASS IV. INSECTA

The body of an insect can be separated into head, thorax, and abdomen. The head is formed of fused segments; it bears four pairs of appendages—one pair of antennæ, one of mandibles, and two of maxillæ. In the thorax there are three segments, each bearing one pair of legs; the second and third segments usually carry a pair of wings on their dorsal surfaces. The abdomen is composed of several (commonly ten) segments, and is usually without appendages. Insects breathe by means of tracheæ.

No undoubted Insects are at present known from the Devonian or earlier formations. But in the Coal Measures and in the Permian the group is represented by a considerable variety of forms. Remains of insects have been found at many horizons in the Mesozoic and Cainozoic formations; in England they are not uncommon in the Lias, the Stonesfield Slate, the Purbeck, the Wealden, and the Bembridge Beds. They are well represented in the Solenhofen Limestone (Upper Jurassic) of Bavaria, in the Miocene of Oeningen in Switzerland and of Florissant in Colorado, and in the amber from the Oligocene Beds of Prussia.

The Insects found in the Palæozoic formations appear to be more generalised than the later forms, and the majority are referred by Handlirsch to Orders distinct from those found in Mesozoic and later periods.

The Insecta include an enormous number of forms, and the specimens found fossil are often imperfectly preserved, so that nothing more than a brief sketch of the distribution of the chief groups can be attempted here.

Apterygota. The fossil examples of this group (which contains small wingless insects) are found mainly in amber from the Oligocene of Prussia, and include several species of *Lepisma* (the silver-fish) and *Machilis.*

The *Palæodictyoptera* are confined to the Carboniferous and Permian, and show primitive and generalised characters; they are believed to be the ancestors of the other groups of winged insects.

Orthoptera. The Forficulidæ (earwigs) appear first in the Eocene, and examples have been found in the Oligocene amber and in the Miocene, but they are not common. In the Coal Measures and Permian the cockroaches (Blattidæ)

are well represented, and the group is fairly common in the Jurassic; the Tertiary forms occur mainly in the Oligocene amber and are all modern types. The Mantidæ ('soothsayers') are found in the Oligocene, and forerunners of this group occur in the Permian and Lias; the Phasmidæ (leaf and stick insects) are present in the Upper Jurassic and Tertiary deposits. The Locustidæ (locusts) are represented in the Lias, in the Upper Jurassic of Solenhofen, and in the Miocene of Oeningen and Florissant. The Gryllidæ (crickets) occur in the Jurassic, the Eocene, the Oligocene amber, and in the Miocene. Orthopterous insects are found in the Coal Measures and the Permian, but since they show characters which connect them with both the Palæodictyoptera and the true Orthoptera they are regarded as constituting a separate group—the Protorthoptera.

The *Isoptera* or Termitidæ (white ants) have been found in the Eocene, Oligocene and Miocene.

The *Ephemeroptera* (Ephemeridæ), known as may-flies, are represented in the Permian, the Jurassic, the Oligocene amber and in the Miocene of Colorado.

The *Paraneuroptera* or *Odonata* (dragon-flies) occur first in the Lower Lias, and are also found in the Stonesfield Slate and the Solenhofen Limestone; in the Eocene and Miocene more advanced types predominate. Forerunners of the dragon-flies (Protodonata) are present in the Coal Measures, the Permian and the Trias, and appear to be intermediate in character between the true dragon-flies and the extinct Palæodictyoptera.

Hemiptera. Insects allied to the Hemiptera, but more generalised in character, are found in the Permian. Forms which can be definitely assigned to this Order appear in the Lias; whilst in the Tertiary deposits most of the modern families are represented. Examples of the Aphidæ

(plant lice) are common in the Eocene, Oligocene and Miocene. Fulgoridæ are found in the Lias, the Purbeck Beds and in the Tertiary. Notonectidæ (water-boatmen) appear in the Upper Jurassic, and also occur in the Oligocene and Miocene.

Neuroptera (lace-wing flies, etc.) are found first in the Lias and are also represented in the Upper Jurassic. Examples belonging to modern families occur in Tertiary deposits.

Trichoptera (caddis-flies) are represented by primitive types in the Lias and Purbeck Beds. Genera belonging to modern groups are found in the Eocene of Wyoming, the Oligocene amber, and in the Miocene of Colorado.

Lepidoptera. Butterflies and moths are very rare as fossils. A few occur in the Middle and Upper Jurassic rocks, *e.g. Palæontina oolitica* from the Stonesfield Slate. The Order is better represented, although still uncommon, in the Tertiary Beds; examples have been found in the Oligocene of the Isle of Wight, the Oligocene amber of the Baltic, and in the Miocene of Colorado.

The *Coleoptera* (beetles) first appear in the Trias; they are more numerous in the Upper Jurassic, and are well represented in some of the Tertiary Beds. Examples have been found in the Lias, the Stonesfield Slate, the Solenhofen Limestone, the Purbeck Beds, the Lower Chalk of Bohemia, the Oligocene amber, and in the Miocene of Oeningen and Colorado.

The *Diptera* include flies, fleas, gnats, and mosquitoes. A few forms are found in the Lias, the Solenhofen Limestone, and the Purbeck Beds; the Order is represented in Tertiary deposits by numerous forms belonging to modern families.

The *Hymenoptera* include ants, bees, wasps, saw-flies,

etc. The earliest examples are found in the Jurassic (Solenhofen Limestone and Purbeck beds), and the Order shows a considerable development in the Cretaceous. A large number of forms are met with in the Tertiary, where most of the important modern families are represented. Ants, wasps and bees are common in the Miocene of Colorado; saw-flies in the Oligocene amber, etc. Hymenoptera have been found in the Oligocene of the Isle of Wight.

CLASS V. ARACHNIDA

Scorpions (fig. 172), spiders, and mites are common forms of the Arachnida. In the members of this Class the anterior segments of the body are fused together, forming a *prosoma* or cephalothorax which is covered by a carapace. This region usually bears six pairs of appendages, of which one pair is in front of the mouth. Antennæ are absent, and no pair of appendages is modified to serve exclusively as jaws. The first and second pairs, known as *cheliceræ* and *pedipalpi*, serve partly as jaws; the four remaining pairs are long limbs, placed near the mouth, and used for locomotion and to some extent as jaws. The abdomen may or may not be segmented; in some groups it is divided into an anterior and a posterior region (*mesosoma* and *metasoma*), each of which consists typically of six segments. The first segment of the mesosoma bears the genital pore. The metasoma bears no appendages, and those on the mesosoma are never in the form of locomotory limbs, but are connected with respiration; in the primitive aquatic arachnids they are plate-like and bear lamellar gills; in the terrestrial forms the gills are replaced by lung-books or by tracheæ.

The Arachnida are divided into two sub-classes:—(1) Merostomata, (2) Euarachnida.

SUB-CLASS I. MEROSTOMATA

The Merostomata are aquatic Arachnids which breathe by means of gills borne on the plate-like appendages of the mesosoma. There are two Orders:—(1) Xiphosura, (2) Eurypterida.

ORDER I. XIPHOSURA

The only living representative of the Xiphosura is the king-crab, *Limulus* (figs. 166, 167), found on the eastern

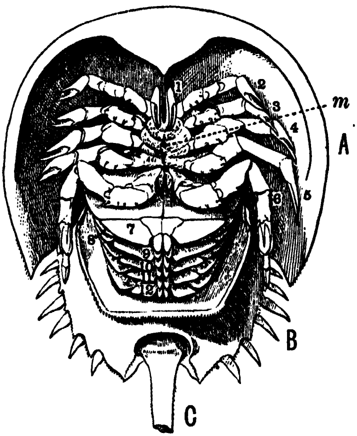


Fig. 166. *Limulus polyphemus*, Recent. Ventral surface. A, cephalothorax or prosoma; B, abdomen; C, portion of the tail-spine. 1—6, appendages of the prosoma; 1, chelicera; 2—6, ambulatory legs—behind the mouth are the small chilaria; 7—12, appendages of the abdomen; 7, operculum; 8—12, lamellar appendages bearing gills; *m*, mouth. Reduced.

shores of North America and Asia, and in the Malay Archipelago and the Indian Ocean. The body of *Limulus* is covered by a chitinous exoskeleton, and consists of a prosoma or cephalothorax (figs. 166, A; 167, 1) and an

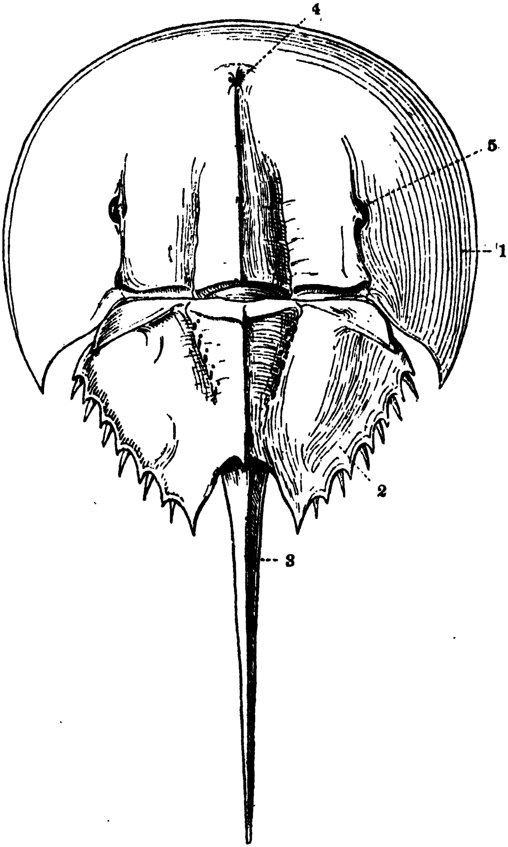


Fig. 167. ***Limulus polyphemus*, Recent. Dorsal view. 1, carapace covering prosoma (cephalothorax); 2, abdominal shield; 3, tail-spine; 4, median eye; 5, lateral eye. (From Shipley and MacBride.) × $\frac{1}{2}$.**

abdomen (figs. 166, B; 167, 2), formed of the mesosoma and metasoma fused together. At the end of the abdomen is a long, movable tail-spine (fig. 167, 3).

The prosoma is covered dorsally by a large crescentic or nearly semicircular carapace (fig. 167, 1), which is very convex above and carries on its upper surface two pairs of eyes, one compound and lateral (5), the other simple and median (4). The large compound eyes are near the middle of the lateral parts of the carapace; the small simple eyes are close together in the middle line, near the anterior margin. The abdomen is more or less hexagonal in outline and is movably articulated with the prosoma; both have two longitudinal furrows on the dorsal surface, dividing a narrow axial part from a broad lateral portion on each side, thus giving a superficial resemblance to a Trilobite. The mesosoma forms the main part of the abdomen and is composed of six fused segments, the segmentation being shown by grooves on the dorsal surface, and by the six movable spines borne on each side. The small posterior part of the abdomen without grooves represents the metasoma.

The prosoma carries six pairs of appendages concealed in the concavity of its under surface; the anterior pair (fig. 166, 1) (*chelicerœ*) only are in front of the mouth and are small, three-jointed appendages with chelæ. The other five pairs (2—6) are the long, six-jointed walking-legs and are placed at the sides of and just behind the mouth; most of them (except the last pair) end in chelæ, and their basal joints (except in the sixth pair) are spinose and function in mastication. Behind the mouth are a pair of small unjointed processes, the *chilaria*, which represent a seventh pair of appendages. The abdomen carries six pairs of plate-like appendages; the anterior pair are united, forming

what is known as the *genital operculum* (7), on the posterior surface of which are the genital openings. The operculum covers the remaining five pairs of appendages, which are not united in the middle, and bear on their posterior faces the leaf-like gills, of which there may be from 150 to 200 on each appendage superposed like the leaves in a book.

From the account given above it will be seen that *Limulus* resembles the scorpions in several respects. In both, the prosoma consists of at least six fused segments, covered dorsally by a carapace which bears a pair of median eyes and a pair of compound eyes. The mesosoma of *Limulus* differs from that of the scorpions in having the segments fused, and the metasoma of the former is much reduced; but in both there is a tail-spine behind the anus. The prosoma bears six pairs of appendages which, in both cases, are similar in form and position. On the mesosoma the genital operculum forms the first pair of appendages; the second pair are the pectines of the scorpions, and the first pair of plates which bear gills in *Limulus*. The next four segments carry lung-books in the scorpions and gill-books in *Limulus*. From these characters, and from the absence of antennæ, it is concluded that *Limulus* is allied to the Scorpionida rather than to the Crustacea as was formerly supposed. The differences between the mesosoma and metasoma of *Limulus* and the scorpions are, to some extent, bridged over by some of the Palæozoic Xiphosura described below.

Limulus appears first in the Trias; it has been found in the Middle Jurassic of Northampton, and is common in the Upper Jurassic of Solenhofen in Bavaria, and is also represented in the Upper Cretaceous and the Oligocene. In the Palæozoic deposits—from Silurian to Permian—several other Xiphosura occur; most of these differ from

Limulus in having some or all of the abdominal segments free, and in some cases the abdomen is clearly separable into mesosoma and metasoma (fig. 168). In these respects the Palæozoic Xiphosura approach both the Eurypterida and the Scorpionida more nearly than does *Limulus*. In most of the Palæozoic specimens the appendages are not preserved. The examples found in the Coal Measures may perhaps have lived in fresh water.

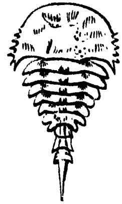


Fig. 168. *Hemiaspis limuloides*, from the Lower Ludlow Beds. × ½.

Belinurus. Form similar to *Limulus*. Prosoma semicircular, with a flat border and long spines from the posterior angles; median part raised, with compound eyes at the sides and median eyes at the front. Mesosoma of five free segments, with the lateral parts produced into spines. Metasoma small, formed of three fused segments with a long tail-spine. Upper Old Red Sandstone and Coal Measures. Ex. *B. reginæ*.

Euproöps (=*Prestwichia*). Prosoma similar to *Belinurus*. Abdominal segments (probably seven) fused, with a flat marginal part produced into spines, and a short tail-spine. Coal Measures. Recorded from the Upper Devonian of Pennsylvania and Permian of Kansas. Ex. *E. danæ*, Coal Measures.

Hemiaspis (fig. 168). Prosoma semicircular, with spines at the external margin and angles; central part raised. Mesosoma of six broad, short, free segments, with the axial part raised; metasoma much narrower, of three segments and a pointed tail-spine. Silurian. Ex. *H. limuloides*.

Bunodes. Similar to *Hemiaspis*. Prosoma without spines. Mesosoma with broad axial part. Metasoma of three or four segments, with a long tail-spine. Silurian. Ex. *B. lunula*.

Neolimulus. Prosoma very broad, rounded in front, with

spinose angles; with median eyes and compound lateral eyes. Abdomen with eight or more free segments, with the axial part tapering rapidly backwards. Silurian. Ex. *N. falcatus.*

Distribution of the Xiphosura

Fossil Xiphosura are rare, except in the Solenhofen Limestone (Upper Jurassic). The earliest form which seems likely to belong to the Xiphosura is *Aglaspis* from the Cambrian of Wisconsin. The chief genera are:

Silurian. *Hemiaspis, Neolimulus, Bunodes, Pseudoniscus.*

Devonian. *Belinurus, Protolimulus.*

Carboniferous. *Belinurus, Euproöps* (=*Prestwichia.*)

Permian. *Euproöps* in Kansas.

Trias to Oligocene and Recent. *Limulus.*

ORDER II. EURYPTERIDA

The Eurypterids are found only in the Palæozoic rocks and are remarkable for the large size which they often attain; one form (*Pterygotus anglicus*) reaches a length of six feet and is the largest Arthropod known. The Eurypterids have a scorpion-like appearance; but, unlike the scorpions, they were all aquatic animals. The body is compressed dorso-ventrally, and is protected by a chitinous exoskeleton (fig. 169) which is covered with small scale-like markings.

The prosoma or cephalothorax consists of the six anterior segments fused together, and is usually quadrate or semicircular in outline. The carapace, which covers the dorsal surface of the prosoma, bears a pair of small, simple eyes near its centre (fig. 169, *e*), and a pair of large, lateral eyes—one at each of the outer front margins or at some little distance from those margins (*d*).

Behind the prosoma come the twelve free and movable segments of the abdomen; in *Pterygotus* (fig. 169) these

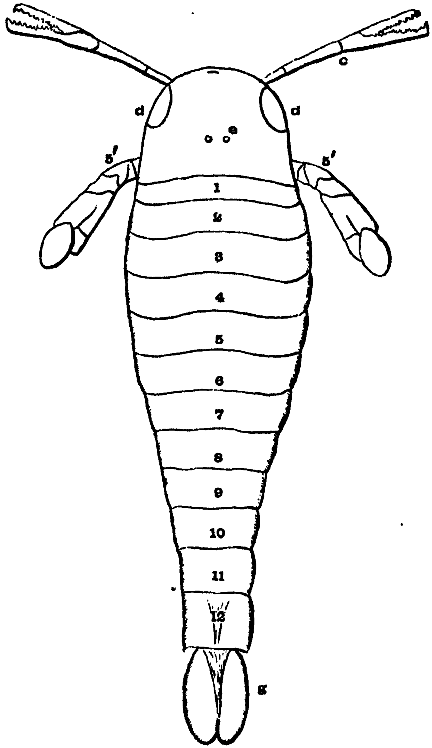


Fig. 169. Dorsal surface of *Pterygotus osiliensis*, from the Upper Silurian, Rootziküll. *c*, first pair of appendages (cheliceræ); *d*, compound eyes; *e*, simple eyes; *g*, tail-plate or 'telson'; 5′, sixth pair of appendages of prosoma; 1—6, segments of the mesosoma; 7—12, segments of the metasoma. Reduced. (After Schmidt.)

segments gradually decrease in width in passing from the anterior to the posterior end, but in many cases (fig. 171) they are divisible into two groups—the anterior segments

being short and broad, whilst the posterior are longer and narrower. The six anterior segments of the abdomen bear

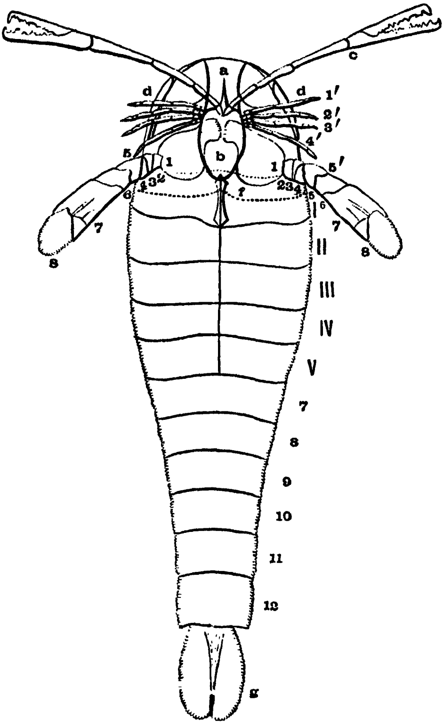


Fig. 170. Ventral surface of *Pterygotus osiliensis*, from the Upper Silurian, Rootziküll. *a*, epistome; *b*, metastoma; *c*, first pair of appendages (cheliceræ), consisting of three joints only (not as shown in the figure), a long basal joint, and two shorter joints forming the chela; *d*, compound eyes; *f*, I, genital operculum; *g*, tail-plate or 'telson'; 1′—5′, second to sixth pairs of appendages; I—V, ventral plate-like appendages of the mesosoma; 7—12, segments of the metasoma. Reduced. (After Schmidt.)

appendages and form the mesosoma (fig. 170, I.—V.; fig. 171, VII.—XII.); the six posterior segments are without appendages and form the metasoma (fig. 170, 7—12; fig.

171, XIII.—XVIII.), at the end of which is the tail-plate or spine (g); this is sometimes (*Eurypterus*) spine-like, but usually in the form of an oval plate which may be produced into a median spine as in *Slimonia,* or divided at the end as in some species of *Pterygotus.* Each segment of the prosoma is covered by a broad, slightly convex dorsal shield (or tergum), and by a ventral cuticle (or sternum), and the tergum of each segment overlaps the one next behind. In the metasoma each segment is surrounded by a continuous chitinous sheath.

The mouth is on the under surface of the prosoma (fig. 171). In front of the mouth there is one pair of appendages only (I.), which end in chelæ and are usually small; each consists of a basal joint (coxa) and two others which form the chela. The other five pairs of appendages (II.—VI.) are at the sides of the elongate mouth; they consist of from six to eight joints each, and are not chelate; they functioned in locomotion, and also in mastication since the inner margins of the basal joints (or coxæ) are provided with tooth-like processes; the posterior pair (VI.), except in *Stylonurus,* are much larger than the others and have a very large basal joint. Placed just behind the mouth, in the median line, is an oval or heart-shaped plate, the *metastoma* (b), which covers the inner parts of the basal joints of the sixth pair of appendages. The metastoma represents the pair of chilaria of *Limulus* (p. 363), and the presence in some cases of a notch in front, and a median longitudinal groove on the surface, supports the view that the metastoma originated from a paired structure. Immediately in front of the mouth another plate, the *epistoma,* is found in *Pterygotus* (fig. 170, a).

The six segments of the mesosoma bear on the ventral surface five pairs of plate-like appendages (fig. 170, I.—V.; fig. 171, VII.—XII.), each of which overlaps the one behind like the tiles on a roof, and on the posterior (or inner) surface of which are the leaf-like gills (fig. 171, *c*). The first pair of plates form the genital operculum, and are divided in the middle by a median process, which often extends beyond the posterior margin of the operculum on to the next pair of appendages; the shape and size of the median process differ in the two sexes. The genital operculum covers the ventral surfaces of both the first and second segments of the mesosoma (fig. 171, VII., VIII.). The segments of the metasoma (figs. 170, 7—12; 171, XIV.—XVIII.) are protected by continuous chitinous rings and bear no appendages.

In many respects the Eurypterids resemble the Scorpions. The number of segments in each of the three regions of the body is the same, and the two pairs of eyes are similar in character and position. In both Eurypterids and Scorpions the prosoma bears six pairs of appendages, of which the first are pre-oral and chelate, and the remaining five agree in position and in general form; but in the Eurypterids the number of joints in the walking legs varies, and the basal segments of all serve as jaws, whereas in the Scorpions the last two pairs function only in locomotion; also in the Eurypterids the last leg and the genital operculum are much larger relatively than in the Scorpions. One of the characteristic features of the Eurypterids is the large metastoma; this is represented by the small sternum of the Scorpions. The pectines are absent in the Eurypterids, except perhaps in *Glyptoscorpius* from the Carboniferous. The lung-books of the Scorpions are represented by the leaf-like gills

of the Eurypterids, but the plate-like appendages of the mesosoma are absent in the Scorpions. In both groups the segments of the metasoma are free and without appendages and at the posterior end is a tail-spine. The differences between the Eurypterids and recent Scorpions are to some extent bridged over by *Palæophonus*, a Silurian Scorpion (see p. 376).

The Eurypterids agree in many respects with *Limulus*. The principal points of difference are :—(1) only the first pair of appendages are chelate in Eurypterids, whereas in *Limulus* all the walking-legs except the last, and the first in the male, may be chelate; (2) the last pair of legs are larger in Eurypterids than in *Limulus* and their basal joints assist in mastication; (3) the large, single plate forming the metastoma in Eurypterids is represented by the pair of small chilaria of *Limulus*; (4) the second segment of the mesosoma in Eurypterids is without appendages and is covered by the genital operculum; (5) in the abdomen all the segments are free in Eurypterids but fused in *Limulus*, and in the latter the metasoma is much reduced—these differences in the abdomen, however, are bridged over by the Palæozoic Xiphosura.

In the Cambrian, Ordovician and Silurian formations Eurypterids are found in marine deposits, but in the Old Red Sandstone they became adapted for life in brackish water and, in some places, in fresh water, and in the Coal Measures they seem to have lived in fresh water only. From the character of their appendages some of the Eurypterids appear to have been adapted for swimming, whilst others were better fitted for crawling. The broad flattened prosoma suggests that most of them were able to burrow in mud and sand in search of food in the same way that *Limulus* does at the present day.

Eurypterus. Prosoma (cephalothorax) quadrate, the anterior angles rounded; the compound eyes are a little in front of the median lateral point on each side. The tail-spine is long, narrow, and pointed. The pre-oral appendages are small and consist of a basal joint and a chela; the second appendage consists of seven joints, the remaining four pairs of eight joints; all these five pairs of appendages are without chelæ. The second, third and fourth pairs are similar in structure and bear spines; the fifth pair are longer than the preceding and without spines; and the sixth pair are much longer and also larger, with a large quadrate basal joint. The metastoma is oval. The median process of the genital operculum is short in the male, long in the female. Ordovician to Permian. Ex. *E. fischeri*, Upper Silurian.

Stylonurus. General form similar to *Pterygotus*. Second, third, and fourth pairs of appendages with spines; the two posterior pairs very long and slender. Compound eyes near the middle of the prosoma. Tail-spine long, pointed. Body sometimes nearly 5 feet long. Upper Silurian and Old Red Sandstone. Recorded from the Ordovician of New York. Ex. *S. powriei*, Upper Silurian and Old Red Sandstone.

Pterygotus (figs. 169, 170).

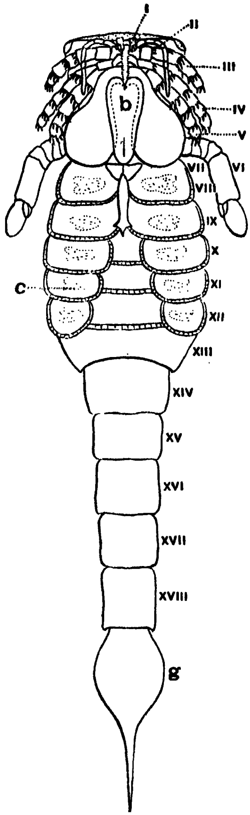


Fig. 171. *Slimonia*. Restoration of the under surface by M. Laurie. *b*, metastoma; *c*, leaf-like gills seen through the ventral plate-like appendages of the mesosoma; *g*, tail-plate; I.—VI., appendages of the prosoma; VII.—XII., segments of the mesosoma; XIII.—XVIII., segments of the metasoma; VII.—VIII., genital operculum. Reduced.

Prosoma rounded in front; the compound eyes are at the margins. The tail-plate is oval and either bilobed or pointed at its extremity. The pre-oral appendages are long and chelate; the second, third, fourth and fifth pairs are similar to each other in size and structure; the sixth pair long and stout. Metastoma oval. The examples of this genus are often of enormous size, *P. anglicus* sometimes reaching a length of 6 feet. Lower Ludlow to Old Red Sandstone. Ordovician of New York. Ex. *P. anglicus*, Old Red Sandstone; *P. bilobus*, Upper Silurian.

Slimonia (fig. 171). Prosoma quadrate; the compound eyes at the anterior angles. Segments of the mesosoma broader than those of the metasoma. The tail-plate is oval, ending in a pointed process or spine. Metastoma heart-shaped. The pre-oral appendages (cheliceræ) are small; the second pair of appendages are slender, and composed of six joints; the third, fourth, and fifth pairs have seven joints, and are similar in size and form; the sixth pair are longer and have a large retort-shaped basal joint. Upper Ludlow and Passage Beds. Ex. *S. acuminata*, Uppermost Silurian.

Distribution of the Eurypterida

This Order ranges from the Cambrian to the Permian, but is most abundant in the Upper Silurian and the Old Red Sandstone. The only form known from the Cambrian is *Strabops*, from Missouri; from the Ordovician, *Eurypterus* and *Echinognathus*. The chief genera in the Silurian and Old Red Sandstone are *Eurypterus*, *Stylonurus*, *Pterygotus*, *Hughmilleria*, and *Slimonia*; and in the Carboniferous and Permian, *Eurypterus*.

SUB-CLASS II. EUARACHNIDA

The Euarachnids breathe air by means of either pulmonary sacs or tracheæ, and the mesosoma is without plate-like appendages. The principal Orders are:—(1) Scorpionida, (2) Pedipalpi, (3) Araneida, (4) Pseudoscorpionida, (5) Phalangidea, (6) Acarina.

ORDER I. SCORPIONIDA

The Scorpions (fig. 172) have a long, narrow body, in which three regions are clearly marked. In front, the *prosoma* or cephalothorax consists of six fused segments, covered dorsally by a chitinous carapace which bears a pair of simple eyes near its centre, and a group of simple eyes at each of the two outer front margins. The middle region of the body—the *mesosoma* or pre-abdomen (7—12) —is formed of six free segments, which are short and broad; the chitinous sheath of each segment consists of a dorsal plate or *tergum* and a ventral plate or *sternum.* The posterior portion of the body is the *metasoma* or post-abdomen (13, 14), and is formed of six segments, each being encased in a complete chitinous cylinder, and all, except the first (13), are narrow; at the end of the last segment is the tail-spine (15), which bears the poison glands. The anal opening is on the last segment.

The prosoma bears six pairs of appendages:—(1) the *chelicerœ* (fig. 172, 1) are small three-jointed limbs with chelæ, placed just in front of the mouth; (2) the *pedipalps* (2) are the largest appendages and are at the sides of the mouth; they consist of six joints, ending with chelæ, and the basal joints function in mastication; next come four pairs of seven-jointed walking legs (3—6) which end in claws, instead of chelæ; the basal joints of the third and fourth pairs assist in mastication. Between the bases of the last two pairs of legs, and immediately in front of the genital operculum, is a small plate, the *sternum.*

On the seventh segment of the body (the *first* of the mesosoma) there is a small rounded plate—the *genital operculum* (fig. 172, 7). The eighth segment bears the *pectines* (8), which are tactile organs and consist of a stem

with a row of short processes like the teeth of a comb. On segments nine to twelve, there are, in the adult, no

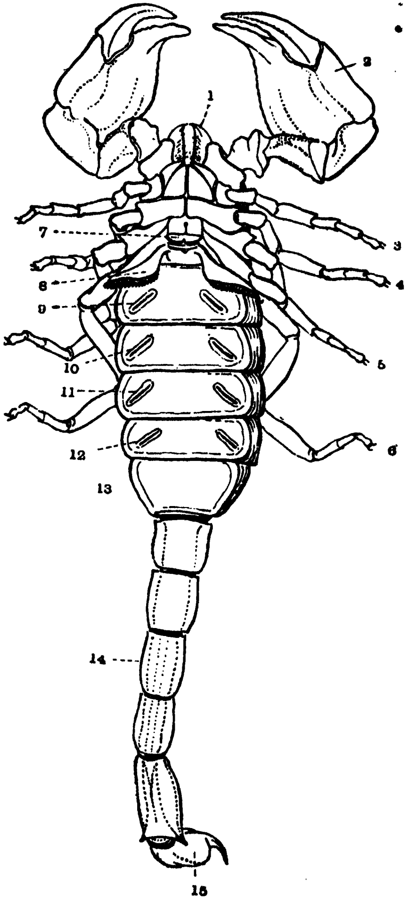


Fig. 172. Ventral view of an Indian Scorpion, *Scorpio swammerdami*. 1, chelicera ; 2, pedipalp ; 3, 4, 5, 6, walking-legs ; 7, genital operculum ; 8, pectines ; 9, 10, 11, 12, the four right stigmata leading to the lung-books ; 13, first segment of metasoma ; 14, fourth segment of metasoma ; 15, tail-spine. (From Shipley and MacBride.) $\times \frac{2}{3}$.

proper appendages; but a pair of oblique, slit-like openings—the *stigmata*, occur on each of these segments, and lead into pulmonary sacs which contain the lung-books. The metasoma (segments 13 to 18) has no appendages.

Although this Order is of great antiquity, it has but few fossil representatives. *Palæophonus* (fig. 173) occurs in the Silurian rocks of Gothland and Lanarkshire; *Proscorpius* in the Silurian of North America. *Eoscorpius*, *Archæoctonus* and *Anthracoscorpio* are found in the Carboniferous. Imperfect specimens of scorpions have been obtained from the Trias of Warwickshire. One form (*Tityus*) is known from the Oligocene beds.

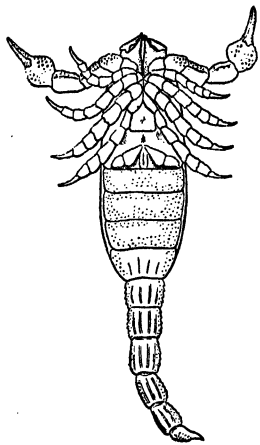


Fig. 173. *Palæophonus caledonicus* from the Upper Silurian of Lesmahago, Lanarkshire. Restoration of ventral surface by R. I. Pocock. $\times 1\frac{1}{2}$.

In some of its characters *Palæophonus* (fig. 173) is more primitive than later scorpions; the walking legs consist of nearly equal-sized joints and seem to be without claws; the basal joints of all these legs could serve to some extent as jaws and in this respect resemble the walking legs of *Limulus* and still more those of the Eurypterida. *Palæophonus*, unlike later scorpions, seems to have been aquatic, since it is found associated with marine fossils, and moreover, stigmata appear to have been absent—probably therefore it breathed by means of branchial lamellæ instead of lung-books.

Of the Carboniferous genera some (*Archæoctonus*, *Anthracoscorpio*) do not differ in any important respect

from living forms and appear to have been as highly organised, but others (*Eobuthus*) show some morphological characters not found in living scorpions.

ORDER II. PEDIPALPI

The Pedipalpi ('whip-scorpions,' etc.) are represented by *Geralinura* and *Græophonus* in the Carboniferous, and by *Phrynus* in the Tertiary rocks.

ORDER III. ARANEIDA

Spiders belonging to the genera *Protolycosa*, *Arthrolycosa*, etc., are found in the Coal Measures. In the Oligocene—especially in the amber of Prussia—a large number of forms occur. Others are found in the Eocene of Wyoming, and the Miocene of Florissant, Colorado.

ORDER IV. PSEUDOSCORPIONIDA (CHERNETIDEA)

This Order includes the 'book-scorpions' (*Chelifer*) and others. Various forms, belonging to existing genera, occur in the Oligocene amber, *e.g.* *Chelifer*, *Chernes*.

ORDER V. PHALANGIDEA (OPILIONINA)

Examples of this Order ('harvest-men,' etc.) have been found in the Oligocene amber. A few forms found in the Carboniferous may belong to this Order.

ORDER VI. ACARINA

This Order comprises the mites and ticks. Various forms of mites, belonging chiefly to living genera, occur in the Oligocene amber and other Tertiary deposits.

ORDER VII. ANTHRACOMARTI

This is an extinct Order, found in the Carboniferous, and appears to be related to the Pedipalpi and Phalangidea. The principal genera are *Brachypyge*, *Anthracomartus*, *Kreischeria*, *Eophrynus*, *Anthracosiro*.

LIST OF PALÆONTOLOGICAL WORKS

ABBREVIATIONS

A. J. S.	American Journal of Science.
A. M. N. H.	Annals and Magazine of Natural History.
G. M.	Geological Magazine.
Q. J. G. S.	Quarterly Journal of the Geological Society.

GENERAL

Zittel, K. A. von. (1) Handbuch der Palæontologie. 1876–93. Also in French.) (2) Grundzüge der Palæontologie. Ed. 2. 1903. (3) and **C. R. Eastman**, Text-book of Paleontology. Ed. 2. 1913.

Bernard, F. Eléments de Paléontologie. 1895.

Neumayr, M. Die Stämme des Thierreiches. 1889.

Depéret, C. The Transformations of the Animal World. 1909.

Osborn, H. F. Palæontology. Encyc. Britt., ed. 11, xx., 1911, p. 579.

McCoy, F. (1) British Palæozoic Fossils. [pp. 1–184, 1851; pp. 185–406, 1852; pp. 407 to end, 1855.] (2) Carboniferous Limestone Fossils of Ireland. 1844. (3) Silurian Fossils of Ireland. 1846.

Murchison, R. I. (1) The Silurian System. 1839. (2) Siluria ed. 5. 1872. [For Lower Palæozoic Fossils.]

Whidborne, G. F. Devonian Fauna of the South of England. 3 vols. 1889–1907. (Palæont. Soc.)

Rœmer, F. and **Frech, F.** Lethæa geognostica. (i) Palæozoica. 1876–1902. (ii) Das Mesozoicum. 1903–13. (iii) Das Cainozoicum. 1903–4.

Koninck, L. G. de. Faune du Calcaire Carbonifère de Belgique. 6 parts. 1878–87.

CATALOGUES OF FOSSILS

Bassler, R. S. Index to American Ordovician and Silurian Fossils (Smithson. Inst. U.S. Nat. Mus., Bull. 92). 1915.

Bigsby, J. J. (1) Thesaurus Siluricus. 1868. (2) Thesaurus Devonico-Carboniferus. 1878.

Bronn, H. G. Index Palæontologicus. 1848.

Etheridge, R. Fossils of the British Islands. (Palæozoic.) 1888.

Etheridge, R., jun. Catalogue of Australian Fossils. 1878.

Miller, S. A. (1) American Palæozoic Fossils. 1877. (2) North American Geology and Palæontology. 1889.

Morris, J. Catalogue of British Fossils. Second edition. 1854.

Sherborn, C. D. Index Animalium. I. 1902.

Catalogues of Type Fossils in the following Museums:—Bath (by *E. Wilson*); Brighton (by *E. Crane*); British Museum (Cephalopoda by *G. C. Crick*, Blastoidea by *F. A. Bather*); Bristol (*E. Wilson*); Cambridge (*H. Woods*); Manchester (*H. Bolton*); Museum of Practical Geology (*H. A. Allen*); Norwich (*F. Leney*); York (*H. M. Platnauer*).

FORAMINIFERA

Brady, H. B. (1) Foraminifera (Challenger Report). 1884. (2) Carboniferous and Permian Foraminifera. 1876. (Palæont. Soc.)

Carpenter, W. B. Introduction to the Foraminifera. 1862.

Chapman, F. The Foraminifera. 1902. With Bibliography.

Gamble, F. W. Radiolaria (Lankester's Treatise on Zoology. I. I., p. 94). 1909.

Jones, T. R., Parker, W. K. and **Brady, H. B.** Crag Foraminifera. 1866, 1895. (Palæont. Soc.)

Lister, J. J. (1) The Foraminifera (Lankester's Zoology. I. 2). 1903. (2) Dimorphism of *Nummulites*. Proc. Roy. Soc., 76 B (1905), p. 298.

Sherborn, C. D. (1) Bibliography of Foraminifera. 1888. (2) Index to Foraminifera. 1893–6. (Smithsonian Miscell. Coll.)

RADIOLARIA

Cayeux, L. Organismes dans le Terrain Pré-cambrien. Bull. Soc. géol. France (3), XXII. (1894), p. 197. Also G. M. (1894), p. 419; and *Rauff*, Neues Jahrb. für Min. etc., I. (1896), p. 116.

Haeckel, E. (1) Die Radiolarien. 1862. (2) Report on the Radiolaria (Challenger Report). 1887.

Hinde, G. J. (1) Ordovician Radiolaria. A. M. N. H. (6), VI. (1890), p. 40. (2) Devonian and Carboniferous Radiolaria. Q. J. G. S. XLIX. (1893), p. 215; *ibid.* LI. (1895), p. 609; *ibid.* LV. (1899), pp. 38, 214.

Holmes, W. M. Chalk Radiolaria. Q. J. G. S., LX. (1899), p. 694. Also *ibid.* LI. (1895), p. 600. G. M. (1895), p. 345.

Rüst. Radiolarien. Palæontographica. (Jurassic) XXXI. (1885), p. 269; (Chalk) XXXIV. (1888), p. 181; (Trias and Palæozoic) XXXVIII. (1892), p. 107; (Jurassic and Chalk) XLV. (1898), p. 1.

PORIFERA

Dendy, A. Sponges. Encyc. Britt., ed. 11, xxv., 1911, p. 715.

Hall, J. and **Clarke, J. M.** Palæozoic Reticulate Sponges (Dictyospongidæ). New York. 1898.

Hinde, G. J. (1) Catalogue of Sponges in the Geological Department of the British Museum. 1883. (2) British Fossil Sponges. 1887–93. (Palæont. Soc.) (3) *Porosphæra.* Journ. R. Micr. Soc. 1904, p. 1.

Kolb, R. Die Kieselspongien des Schwabischen Weissen Jura. Palæontographica, LVII., 1910.

Minchin, E. A. Sponges. (Lankester's Zoology, II.) 1900.

Polejaeff, N. E. Calcarea (Challenger Report). 1883.

Rauff, H. (1) Palæospongologie. Palæontographica, XL., 1893–4; XLI. (1895), p. 223. (2) Receptaculitidæ. Abhandl. der math.-phys. Classe d. k. bayer. Akad. XVII. (1892), p. 645.

Ridley, S. O. and **Dendy, A.** Monaxonida (Challenger Report). 1887.

Schrammen, A. Die Kieselspongien d. oberen Kreide N.W. Deutschland. Palæontographica, Suppl.-Bd. v. 1910–12.

Schultze, F. E. Hexactinellida (Challenger Report). 1887.

Sollas, W. J. Tetractinellida (Challenger Report). 1888.

GRAPTOLITOIDEA

Allman, G. J. Morphology and Affinities of Graptolites. A. M. N. H. (4), IX. (1872), p. 364.

Barrande, J. Graptolites de la Bohême. 1850.

Elles, G. L., Wood, E. M. R. and **Lapworth, C.** British Graptolites. 1901–14. (Palæont. Soc.)

Hall, J. Graptolites of the Quebec group. 1865.

Hermann, O. Distribution, Organisation and Economy of Graptolithidæ. G. M. (1885), pp. 406, 448. Dichograptidæ, *ibid.* (1886), p. 13.

Holm, G. (1) On *Didymograptus*, *Tetragraptus*, and *Phyllograptus.* G. M. (1895), pp. 433, 481. (2) Gotlands Graptoliter. Bih. K. Svenska Vet. Akad. XVI. no. 7 (1890).

Hopkinson, J. (1) Morphology of Rhabdophora. A. M. N. H. (5), IX. (1882), p. 54. (2) Reproduction, *ibid.* (4), VII. (1871), p. 317.

Lapworth, C. (1) Distribution of Rhabdophora. A. M. N. H. (5), III. (1879), pp. 245, 449; IV. (1879), pp. 333, 423; V. (1880), pp. 45, 273, 358; VI. (1881), pp. 16, 185. (2) Classification of Rhabdophora. G. M. Vol. x. (1873), pp. 500, 555.

Nicholson, H. A. and **Marr, J. E.** Phylogeny of Graptolites. G. M. (1895), p. 529.

Perner, J. Graptolites de la Bohême. Parts I.—III., 1894–99.

Ruedemann, R. (1) Development and Mode of Growth of *Diplograptus*. 14th Ann. Rep. State Geol. New York for 1894 (1895), p. 219. Also A. J. S. ser. 3, XLIX. (1895), p. 453. (2) Graptolites of New York, Part I., 1904; Part II., 1908. (N. York State Mus. Mem. 7.)

Törnquist, S. L. (1) Structure of Diprionidæ. Säртryck af Konl. Fysiogr., Handl. Ny Följd, IV. 1893. (2) Graptolites of *Phyllo-Tetragraptus* Beds. Konl. Fysiogr. Sällsk. Handl. XII. (1901).

Walther, J. Die Lebensweise der Graptolithen. Zeitschr. der deutsch. geol. Gesellsch. XLIX. (1897), p. 238.

Wiman, C. Diplograptidæ and Monograptidæ. Bull. Geol. Inst. Upsala, I. (1894), pp. 97, 113; also Nat. Sci. IX. (1896), pp. 186, 240.

STROMATOPOROIDEA

Heinrich, M. Structure and Classification of Stromatoporoidea. Journ. Geol. XXIV. (1916), p. 57.

Nicholson, H. A. British Stromatoporoidea. 1886–92. (Palæont. Soc.)

Parks, W. A. Niagara, Ordovician and Silurian Stromatoporoids. Univ. Toronto Studies, Geol. Series, 5, 6, 7. 1908–10.

Törnquist, A. Ueber mesozoische Stromatoporiden. Sitzung. k. preuss. Akad. Wissensch. Berlin 1901, p. 1115. Also *Bakalow*, Neues Jahrb. für Min. etc. (1906), I. p. 13; *Deninger*, *ibid.* p. 61.

SCYPHOMEDUSÆ

Maas, O. Ueber Medusen aus dem Solenhofer Schiefer und der Kreide. Palæontographica, XLVIII. (1902), p. 297.

Walcott, C. D. (1) Fossil Medusæ. Mon. U. S. Geol. Survey, XXX. 1898. (2) Cambrian Geology and Palæontology, II. (1911), p. 55.

ANTHOZOA (ACTINOZOA)

Beecher, C. E. (1) Development of a Palæozoic Poriferous Coral. Trans. Connecticut Acad., VIII. (1893), p. 207. (2) Development of Favositidæ, *ibid.* p. 215. *Girty*, Amer. Geol. XV. (1895), p. 131.

Bernard, H. M. *Alveopora* and the Favositidæ. Journ. Linn. Soc. (Zool.) XXVI. (1898), p. 495.

Bourne, G. C. (1) The Anthozoa (Lankester's Zoology, Part II.), 1900. (2) *Heliopora* etc. Phil. Trans. Roy. Soc. CLXXXVI. (1895), p. 455.

Brook, G. and **Bernard, H. M.** Catalogue of Madreporarian Corals in the British Museum. I.—IV. 1893–1903.

Brown, T. C. Development of *Streptelasma*. A. J. S. (4), XXIII. (1907), p. 277.

Carruthers, R. G. (1) Septal Plan of the Rugosa. A. M. N. H. (7), XVIII. (1906), p. 356. (2) Revision of Carboniferous Corals. . G. M. (1908), pp. 20, 63.

Dana, J. D. Zoophytes. (Wilkes Expedition), 1848.

Duerden, J. E. (1) Morphology of Madreporaria. Septal Sequence. Biol. Bull., VII. (1904), p. 79; IX. (1905), p. 27. (2) Relationships of Rugosa to Zoantheæ. A. M. N. H. (7), IX. (1902), p. 381.

Duncan, P. M. (1) British Fossil Corals. 1866–72. (Palæont. Soc.) (2) Revision of the Families and Genera of the Madreporaria. Journ. Linn. Soc. (Zool.) XVIII. (1885), pp. 1-204.

Dybowski, W. N. Monographie der Zoantharia Rugosa, etc. Arch. für Naturk. Liv-, Est- und Kurlands. V. 1874.

Edwards, H. Milne. (1) Histoire naturelle des Coralliaires. 1857–60. (2) and **Haime, J.** British Fossil Corals. 1850–54. (Palæont. Soc.)

Felix, J. Die Anthozoen der Gosauschichten. Palæontographica, XLIX. (1903), p. 163.

Frech, F. (1) Die Korallenfauna der Trias. Palæontographica, XXXVII. (1890), p. 1. (2) Die Korallenfauna des Oberdevons in Deutschland. Zeitschr. der deutsch. geol. Gesellsch. XXXVII. (1885), pp. 21, 946.

Fromentel, E. de. Introduction à l'étude des Polypiers fossiles. 1858-61.

Gordon, C. E. Early Stages in Palæozoic Corals. A. J. S. (4), XXI. (1906), p. 109.

Gregory, J. W. Jurassic of Cutch. II. Corals (Palæont. Indica), 1900.

Hickson, S. J. *Tubipora.* Q. J. Micr. Science, XXIII. (1883), p. 556.

Hinde, G. J. *Archæocyathus*, etc. Q. J. G. S., XLV. (1889), p. 125.

Kiär, J. (1) Korallenfaunen des norwegischen Silursystems. Palæontographica, XLVI. (1899), p. 1. (2) Mittelsilurischen Heliolitiden. Skrift. Videns.-Selsk. i Christiana, I. 10. 1903.

Koby, F. (1) Polypiers jurassiques de la Suisse (Mém. Soc. Pal. Suisse). 1881–95. (2) Polypiers crétacés de la Suisse (*ibid.*). 1896–7.

Kunth, A. Foss. Korallen. Zeitsch. d. deutsch. geol. Gesellsch. XXI. (1869), p. 647.

Lang, W. D. Growth Stages in *Parasmilia.* Proc. Zool. Soc., 1909, p. 285.

Lindström, G. Heliolitidæ. Kon. Svensk. Vet. Akad. Handl., XXXII. No. 1 (1899). *Gregory*, Proc. Roy. Soc., LXVI. (1900), p. 291.

Nicholson, H. A. (1) Tabulate Corals of the Palæozoic Period. 1879. (2) *Tubipora* and *Syringopora.* Proc. Roy. Soc. Edin., XI. (1880–81), p. 219. (3) and **J. Thomson.** Study of the chief types of Palæozoic Corals. A. M. N. H. ser. 4, XVI. (1875), pp. 305, 424; XVII. (1876), pp. 60, 123, 290, 451; XVIII. (1876), p. 68.

Ogilvie, M. M. (1) Microscopic and systematic study of Madreporarian Corals. Phil. Trans. Roy. Soc., CLXXXVII. (1896), p. 83. 'Nature,' LV. (1897), p. 280. (2) Q. J. Micr. Sci., LI. (1907), p. 473. (3) Korallen. der Stramberger Schichten. Palæontographica, Suppl. III. 1897.

Ortmann, A. Die Morphologie des Skelettes der Steinkorallen. Zeitschr. für wiss. Zool., L. (1890), p. 278. Neues Jahrb. für Min. etc. (1887) II. p. 185.

Quelch, J. J. Report on Reef Corals (Challenger Report). 1886.

Rominger, C. Fossil Corals. Geol. Surv. Michigan. III. 1876.

Sardeson, F. W. Ueber die Beziehungen der fossilen Tabulaten zu den Alcyonarien. Neues Jahrbuch für Min. etc. X. (1896), p. 249. *Weissermel*, Zeitschr. der deutsch. geol. Gesellsch., XLIX. (1897), p. 368, and L. (1898), p. 54. *Janensch, ibid.* LV. (1903), p. 486.

Schlüter, C. Anthozoen des rheinischen Mittel-Devon. Abhandl. d. preuss. geol. Landes-Anst. VIII. 1889.

Smith, S. (1) *Aulophyllum.* Q. J. G. S., LXIX. (1913), p. 51. (2) *Lonsdaleia, ibid.* LXXI. (1916), p. 218. (3) *Aulina, Phillipsastræa, Orionastræa, ibid.* LXXII. (1917), p. 280.

Vaughan, T. W. Eocene and Oligocene Coral Faunas of the United States. Mon. U. S. Geol. Survey, XXXIX. 1900.

Wentzel, J. Zoantharia Tabulata. Denkschr. d. k. Akad. Wissensch. Math.-nat. Cl. Wien, LXII. (1895), p. 479.

Wright, E. P. and **Studer, T.** Alcyonaria (Challenger Report). 1889.

ECHINODERMA

General

Bather, F. A., Gregory, J. W. and **Goodrich, E. S.** The Echinoderma. (Lankester's Zoology, III.) 1900. *Bather*, Encyc. Britt., ed. 11, VIII., 1910, p. 871.

Clark, W. B. and **Twitchell, M. W.** Mesozoic and Cenozoic Echinodermata of the United States. Mon. U. S. Geol. Surv., LIV. 1915.

Delage, Y. and **Hérouard.** Zoologie Concrète. III. Echinodermes. 1903.

Eleutherozoa

Agassiz, A. (1) Revision of the Echini. Mem. Mus. Comp. Zool. III. 1872–4. (2) Panamic Deep Sea Echini, *ibid.* XXXI. 1904. (3) Echinoidea (Challenger Report). 1881.

Bather, F. A. Triassic Echinoderms of Bakony. 1909.

Cotteau, G. and **Triger.** Échinides de la Sarthe. 1855–69.

Desor, E. (1) Synopsis des Échinides fossiles. 1858. (2) and **de Loriol, P.** Échinologie Helvétique. Jurassique. 1868–72.

Duncan, P. M. (1) Structure of the Ambulacra of fossil Regular Echinoidea. Q. J. G. S., XLI. (1885), p. 419. (2) Revision of the Genera of the Echinoidea. Journ. Linn. Soc. (Zool.), XXIII. (1889), p. 1.

Etheridge, R., jun. Holothuroidea in the Carboniferous. Proc. Roy. Phys. Soc. Edinburgh, vi. (1880–81), p. 183.

Fortau, R. Catalogue des Invertébrés fossiles de l'Égypte. Échinides Éocènes, 1913. Échinodermes Crétacés, 1914.

Forbes, E. (1) Asteriadæ in British Strata. (Mem. Geol. Survey. Organic Remains, dec. i.) 1849. (2) Echinodermata of the British Tertiaries. 1852. (Palæont. Soc.)

Gregory, J. W. (1) British Cainozoic Echinoidea. Proc. Geol. Assoc., xii. (1891), p. 16. (2) Echinothuridæ. Q. J. G. S., liii. (1897), p. 112. (3) *Lindstromaster*, etc. G. M. (1899), p. 341. (4) Palæozoic Ophiuroidea. Proc. Zool. Soc. (1896), p. 1028.

Hawkins, H. L. Holectypoida. Proc. Zool. Soc. (1912), p. 440; and G. M., 1917, pp. 160, 196, 249, 342, 389, 433.

Jackson, R. T. Phylogeny of Echini, with a revision of Palæozoic species. Mem. Boston Soc. Nat. Hist., vii. 1912.

Lambert, J. (1) Échinides de l'Infra-Lias et du Lias. Bull. Soc. Sci. de l'Yonne, liii. (1900), p. 3; (2) and **P. Thiéry,** Essai de Nomenclature raisonnée des Échinides, 1909–10.

Loriol, P. de. Échinologie Helvétique. Crétacé. 1873.

Lovén, S. (1) Echinologica. Bihang Kon. Svensk. Vetenskaps-Akad. Handl. xviii. (4). 1892. (2) Études sur les Echinoides. Kon. Svenska Vet. Akad. Handl. xi. No. 7. 1874.

Lyman, T. Ophiuroidea (Challenger Report). 1882.

Orbigny, A. d'. Paléontologie française. Terr. crét., vi. Échinides irréguliers. 1855–60. Continued by **Cotteau.** vii. Echinides réguliers. 1862–7. Terr. jurassiques, ix. Échinides irréguliers. 1867–74. xi. Échinides réguliers. 1882–89.

Pomel, A. Classification des Échinides. 1883.

Rowe, A. W. *Micraster*. Q. J. G. S., lv. (1899), p. 494.

Sladen, W. P. (1) Asteroidea (Challenger Report). 1889. (2) and **Spencer, W. K.** British Fossil Echinodermata. ii. Cretaceous Asteroidea and Ophiuroidea. 1891–1908. (Palæont. Soc.)

Sollas, W. J. (1) Silurian Echinoidea and Ophiuroidea. Q. J. G. S., lv. (1899), p. 692. (2) *Lapworthura*, Phil. Trans., B, ccii. (1912), p. 213.

Spencer, W. K. (1) Evolution of the Cretaceous Asteroidea. Phil. Trans., B, cciv. (1913) p. 99. (2) British Palæozoic Asterozoa. 1914— (Palæont. Soc.)

Stürtz, B. Beiträge zur Kenntniss palæozoischer Seesterne. Palæontographica, xxxii. (1886), p. 75; xxxvi. (1890), p. 203.

Wright, T. (1) British Oolitic Echinodermata. i. Echinoidea (1857–1878). ii. Asteroidea and Ophiuroidea (1863–1880). (2) British Cretaceous Echinodermata. i. Echinoidea. 1864–1882. (Palæont. Soc.)

Pelmatozoa

Bather, F. A. (1) British Fossil Crinoids. A. M. N. H. (6), v. (1890), pp. 306, 373, 485; vi. (1890), p. 222; vii. (1891), pp. 35, 389; ix. (1892), pp. 189–202. (2) Terms in Crinoid Morphology, *ibid.* ix. (1892), p. 51. (3) Crinoidea of Gothland. Part i. K. Vet. Akad. Handl. (Stockholm), xxv. 1893. (4) *Uintacrinus.* Proc. Zool. Soc. (1895), p. 974. (5) *Petalocrinus.* Q. J. G. S., liv. (1898), p. 401. (6) Studies in Edrioasteroidea, i.–ix. 1915, reprinted from G. M., 1898–1915.

Billings, E. Cystideæ of the Lower Silurian Rocks of Canada. (Geol. Survey of Canada: Organic Remains, dec. iii.) 1858.

Buch, L. von. Ueber Cystideen. Abhandl. d. k. Akad. d. Wiss. zu Berlin (1844), p. 89.

Carpenter, P. H. (1) Crinoidea (Challenger Report). 1884–8. (2) Oral and Apical Systems of Echinoderms. Q. J. Micr. Science, xviii. (1878), p. 351; xix. (1879), p. 176. (3) Morphology of Cystidea. Journ. Linn. Soc. (Zool.), xxiv. (1894), p. 1. (4) and **Etheridge, R.** Catalogue of Blastoidea in the British Museum. 1886.

Forbes, E. Cystidea of the Silurian Rocks of the British Islands. (Mem. Geol. Survey, Vol. ii., Part ii.) 1848.

Jaekel, O. Stammesgeschichte der Pelmatozoen. i. Thecoidea und Cystoidea. 1899.

Koninck, L. de and **Le Hon, H.** Crinoides du Terrain carbonifère de la Belgique. 1854.

Waagen, W. and **Jahn, J. J.** In Barrande's Système Silurien du centre de la Bohême. ii. 1, Cystidées. 2, Crinoides. 1887–99.

Wachsmuth, C. and **Springer, F.** (1) Revision of the Palæocrinoidea. Proc. Acad. Nat. Sci., Philadelphia, 1879, p. 226; 1881, p. 177; 1885, p. 225; 1886, p. 64. (2) *Crotalocrinus, ibid.* 1888, p. 364. (3) North American Crinoidea Camerata. Mem. Mus. Zool. Harvard, xx., xxi., 1897. (4) Springer, *Uintacrinus, ibid.* xxv., 1901.

BRACHIOPODA

Barrande, J. Système Silurien de la Bohême. v. 1879.

Beecher, C. E. Development and Classification of Brachiopoda. 'Studies in Evolution' (1901), pp. 229–415.

Bittner, A. Brachiopoden der Alpinen Trias. Abhandl. d. kk. geol. Reichsanstalt. xiv., 1890. xvii., 1892.

Davidson, T. (1) British Fossil Brachiopoda. 6 vols. 1851–1886. (Palæont. Soc.) (2) Monograph of Recent Brachiopoda. Trans. Linn. Soc. (Zool.), (2), iv., 1886–88.

Deslongchamps, E. Sur le développement du deltidium. Bull. Soc. géol. de France, (2), xix. (1862), p. 409.

Fischer, P. Manuel de Conchyliologie. 1887. [Brachiopods, by Œhlert.]

Fischer, P. and **Œhlert, D. P.** Sur l'évolution de l'appareil brachial de quelques Brachiopodes. Comptes Rendus, cxv. (1892), p. 749.

Friele, H. Development of the Skeleton in *Waldheimia.* Arch. Math. Nat., II. (1877), p. 380.

Hall, J. and **Clarke, J. M.** (1) Introduction to the Palæozoic Brachiopoda. (Geol. Surv. New York, Palæontology. VIII.) I., 1892. II., 1894. (2) Introduction to the study of the Brachiopoda. 1894.

Reed, F. R. C. Ordovician and Silurian Brachiopoda of Girvan. Trans. Roy. Soc. Edinburgh, LI. (1917), p. 795.

Schuchert, C. (1) Classification of the Brachiopoda. American Geologist, XI. (1893), p. 141; XIII. (1894), p. 80. (2) Synopsis of American Fossil Brachiopoda (Bull. U. S. Geol. Surv.). 1897. (3) Paleogeographic and Geologic Significance of Recent Brachiopoda. Bull. Geol. Soc. America, XXII. (1911), p. 258.

Thomas, I. (1) British Carboniferous Orthotetinæ (Mem. Geol. Surv. Gt. Britain, 1910). (2) British Carboniferous Producti (*ibid.* 1914).

Walcott, C. D. Cambrian Brachiopoda (Mon. U. S. Geol. Surv. LI.). 1912.

CHÆTOPODA

Hinde, G. J. Annelid Jaws from the Palæozoic. Q. J. G. S., XXXV. (1879), p. 370. *Ibid.* XXXVI. (1880), p. 368.

POLYZOA

Brydone, R. M. Chalk Polyzoa, G. M. 1906–18.

Busk, G. (1) Polyzoa (Challenger Report). 1884–86. (2) The Crag Polyzoa. 1859. (Palæont. Soc.)

Canu, F. and **R. S. Bassler.** Synopsis of American early Tertiary Cheilostome Bryozoa. Smithsonian Inst., U. S. National Mus. Bulletin 96, 1917.

Cumings, E. R. Development of *Fenestella.* A. J. S. (4), XX. (1905), p. 169.

Gregory, J. W. (1) British Palæogene Bryozoa. Trans. Zool. Soc., XIII. (1893), p. 219. (2) Catalogue of Fossil Bryozoa in the British Museum: Jurassic. 1896. (3) Ditto: Cretaceous. 1899, 1909.

Haime, J. Bryozoaires de la formation jurassique. Mém. Soc. géol. France (2), v. (1854), p. 156.

Hincks, T. History of the British Marine Polyzoa. 1880.

Lang, W. D. (1) Exhibits of Polyzoa in the British Museum. Proc. Geol. Assoc., XXIV., 1913, p. 169. (2) Calcium Carbonate and Evolution in Polyzoa. G. M., 1916, p. 73. (3) Cribrimorph Cretaceous Polyzoa. A. M. N. H. (8), XVIII. 1917, pp. 81, 381.

Nicholson, H. A. Structure and Affinities of *Monticulipora*, etc. 1881.

Orbigny, A. d'. Paléontologie française. Terr. crét. v. 1850–52.

Pergens, E. Revision des Bryozoaires du Crétacé figurés par d'Orbigny. 1. Cyclostomata. Ann. Soc. géol. Belg. Mém., Hydr. III. (1889), p. 305.

Shrubsole, G. W. (1) Carboniferous Fenestellidæ. Q. J. G. S., XXXV. (1879), p. 275. (2) Silurian Fenestellidæ. *Ibid.* XXXVI. (1880), p. 241.

Ulrich, E. O. Lower Silurian Bryozoa of Minnesota. *Geol. and Nat. Hist. Surv. Minnesota, III. (1), 1895, p. 96.

Vine, G. R. Reports on Fossil Polyzoa. Rep. Brit. Assoc. 1880–92.

MOLLUSCA

1. *General*

Adams, H. and **A.** Genera of Recent Mollusca. 3 vols. 1858.

Carpenter, W. Microscopic Structure of Shells. Rep. Brit. Assoc. for 1844 (1845), p. 24; for 1847 (1848), p. 93.

Cossmann, M. Catalogue illustré des Coquilles fossiles de l'Éocène des environs de Paris. Vols. I.–V. 1886–92.

Fischer, P. Manuel de Conchyliologie. 1887.

Morris, J. and **Lycett, J.** Great Oolite Mollusca. 1850–63. (Palæont. Soc.)

Newton, R. B. List of the Edwards Collection of British Oligocene and Eocene Mollusca in the British Museum. 1891.

Pelseneer, P. Mollusca. (Lankester's Zoology, V.) 1907.

Sowerby, J. Mineral Conchology of Great Britain. 7 vols. 1812–46.

Wood, S. V. Crag Mollusca. 2 vols. 1848, 1850, and supplements. (Palæont. Soc.)

Woodward, S. P. Manual of the Mollusca. Edition 4 by Tate. 1880.

2. *Lamellibranchia*

Amalitzky, W. Ueber die Anthracosien der Permformation Russlands. Palæontographica, XXXIX. (1892), p. 125.

Barrande, J. Système Silurien de la Bohême. VI. 1882.

Bernard, F. (1) Le développement et la morphologie de la coquille chez les Lamellibranches. Bull. Soc. géol. de France (3), XXIII. (1895), p. 104; XXIV. (1896), pp. 54, 412; XXV. (1897), p. 559. (2) La coquille des Lamellibranches. Ann. Sci. Nat. (Zool.) (8), VIII. 1898.

Beushausen, L. Die Lamellibranchiaten des rheinischen Devon. Abhandl. d. kk. preuss. geol. Landes-Anst. XVII. 1895.

Cossmann, M. and **G. Pissaro.** Iconographie des Coquilles de l'Éocène de Paris. I. Pélécypodes. 1904–6.

Dall, W. H. (1) The Hinge of Pelecypods. A. J. S. (3), XXXVIII. (1889), p. 445. (2) Classification of Pelecypoda. Trans. Wagner. Inst. Sci. Philadelphia. III. 1895.

Frech, F. Die devonischen Aviculiden Deutschlands. Abhandl. geol. Specialkarte von Preussen. IX. 1891.

Hind, W. (1) *Carbonicola, Anthracomya,* and *Naiadites.* 1894. (2) British Carboniferous Lamellibranchiata. 1896–1905. (Palæont. Soc.)

Jackson, R. T. Phylogeny of the Pelecypoda. The Aviculidæ and their allies. Mem. Boston Soc. Nat. Hist. IV. (1890), p. 277.

Lycett, J. British Fossil Trigoniæ. 1872–79. (Palæont. Soc.)

Neumayr, M. Morpholog. Eintheilung der Bivalven. Denkschr. der k. Akad. der Wissensch. math.-nat. Classe (Wien). LVIII. (1891), p. 701.

Orbigny, A. d'. Paléontologie française. Terr. crét. III. Lamellibranches. 1843–47.

Smith, E. A. Lamellibranchiata (Challenger Report). 1885.

Stoliczka, F. Cretaceous Fauna of S. India. III. Pelecypoda (Palæontologia Indica). 1870–1871.

Wood, S. V. Eocene Bivalves of England. 1861–71. (Palæont. Soc.)

Woods, H. Cretaceous Lamellibranchia of England. 2 vols. 1899–1908. (Palæont. Soc.)

Vest, W. Ueber die Bildung und Entwicklung des Bivalven-Schlosses. Verhandl. u. Mittheil. siebenbürg. Vereins. XLVIII. (1898), p. 25.

Zittel, K. A. Die Bivalven der Gosaugebilde. Denkschr. d. k. Akad. d. Wissensch. XXIV. (2) (1865), p. 105 ; XXV. (2) (1866), p. 77.

3. *Gasteropoda*

Cossmann, M. Essais de Paléoconchologie comparée. 9 parts. 1895–1912.

Donald, J. *Murchisonia,* etc. Q. J. G. S., LI. (1895), p. 210 ; XLIII. (1887), p. 617 ; LIV. (1898), p. 45 ; LV. (1899), p. 251 ; LVIII. (1902), p. 313 ; LXI. (1905), pp. 564, 567 ; LXII. (1906), p. 552.

Grabau, A. W. (1) Studies of Gastropoda. American Naturalist, XXXVI. (1902), p. 917 ; XXXVII. (1903), p. 515 ; XLI. (1907), p. 607. (2) Phylogeny of *Fusus* etc. Smithson. Miscell. Coll., XLIV. (1904), p. 157.

Harmer, F. W. Pliocene Mollusca of Great Britain. 1914–19. (Palæont. Soc.)

Hudleston, W. H. (1) British Inferior Oolite Gasteropoda. 1887–96. (Palæont. Soc.) (2) and **Wilson, E.** Catalogue of British Jurassic Gasteropoda. 1892.

Koken, E. Ueber die Entwickelung der Gastropoden vom Cambrium bis zur Trias. Neues Jahrb. für Min. etc. VI. (1889), p. 305.

Lindström, G. Silurian Gasteropoda and Pteropoda of Gotland. 1884.

Pelseneer, P. Pteropoda (Challenger Report). 1888.

Perner, J. Système Silurien de la Bohême. IV. Gastéropodes. 1903.

Rochebrune, A. T. de. Monog. des espèces foss. des. Polyplaxiphores. Ann. Sci. geol. XIV. (1883), p. 1.

Ulrich, E. O. and **Scofield, W. H.** Lower Silurian Gasteropoda of

Minnesota. (Rep. Geol. and Nat. Hist. Surv. Minnesota, III., 2.) 1897.

Watson, R. B. Scaphopoda and Gasteropoda (Challenger Report). 1886.

Wilson, E. British Liassic Gasteropoda. G. M. (1887), pp. 193, 258.

Zittel, K. A. Die Gastropoden der Stramberger Schichten. (Palæont. Mittheil.) 1873.

4. *Conularia, Hyolithes, etc.*

Holm, G. Sveriges Kambrisk-Siluriska Hyolithidæ och Conularidæ. Sveriges Geol. Undersök. Ser. C. No. 112. Stockholm, 1893.

Novák, O. Revision der palæozoischen Hyolithiden Böhmens. Abhandl. der böhm. Gesellschaft der Wissensch. IV. 1891.

Ruedemann, R. A sessile *Conularia.* Amer. Geol. XVII. (1896), p. 158; XVIII. (1896), p. 65.

Slater, I. L. British Conulariæ. 1907. (Palæont. Soc.)

Želizko, J. V. *Hyolithes.* Centralbl. für Min. etc. (1908), p. 362.

5. *Scaphopoda*

Gardner, J. S. Cretaceous Dentaliidæ. Q. J. G. S., XXXIV. (1878), p. 56.

Newton, R. B. and **Harris, G. F.** British Eocene Scaphopoda. Proc. Malacol. Soc. I. (1894), p. 63.

Richardson, L. Liassic Dentaliidæ. Q. J. G. S., LXII. (1906), p. 573.

6. *Cephalopoda*

Appellöf, A. Die Schalen von *Sepia, Spirula* und *Nautilus.* Kon. Sven. Vetenskaps-Akad. Handl. XXV. 7 (1893).

Barrande, J. Système Silurien du centre de la Bohême. II. (in 6 parts). Céphalopodes. 1867–70.

Blake, J. F. British Fossil Cephalopoda. Part I. Silurian. 1882.

Branco, W. Entwickelungsgeschichte der fossilen Cephalopoden. Palæontographica. XXVI. (1879), p. 19; XXVII. (1880), p. 17.

Buckman, S. S. Inferior Oolite Ammonites. 1887–1907. (Palæont. Soc.)

Crick, G. C. (1) Muscular Attachment in Ammonoidea. Trans. Linn. Soc. (Zool.), ser. 2, VII. (1898), p. 71. (2) *Belemnites.* Proc. Malacol. Soc. II. (1896), p. 117; VII. (1907), p. 269.

Foord, A. H. (1) Carboniferous Cephalopoda of Ireland. 1897–1903. (Palæont. Soc.) (2) and **Crick.** Catalogue of the Fossil Cephalopoda in the British Museum. Parts I.–III. 1888–97.

Frech, F. Ueber devonische Ammoneen. Beitr. z. Geol. Österr.-Ung. u. d. Orients. XIV. 1902.

Grossouvre, A. de. Les Ammonites de la Craie supérieure. (Mém. explicat. Carte géol. de la France.) 1893.

Haug, E. Études sur les Goniatites. Mém. Soc. géol. de France, Paléont. 18. 1898.

Holm, G. Organisation einiger silurischer Cephalopoden. Palæont. Abhandl. III. 1885.

Huxley, T. H. Structure of Belemnitidæ. (Mem. Geol. Survey.) 1864.

Hyatt, A. (1) Fossil Cephalopods. Bull. Mus. Comp. Zool. Harvard. III. no. 5. 1872. (2) Genesis of Arietidæ. Smithsonian Contrib. XXVI. 1889. (3) Phylogeny (chiefly Nautiloidea). Proc. Amer. Phil. Soc. XXXII. (1894), p. 349.

Könen, A. v. Ammonitiden d. norddeutsch. Neocom. Abhandl. d. preuss. geol. Landesanst. XXIV. 1902.

Mojsisovics von Mojsvár, E. (1) Die Cephalopoden der mediterranen Triasprovinz. Abhandl. d. kk. geol. Reichsanst. X. 1882. (2) Die Cephalopoden der Hallstätter Kalk. *Ibid.* VI., i. 1873 ; ii. 1893.

Neumayr, M. I. Jura Studien. Ueber Phylloceraten. Jahrb. d. kk. geol. Reichsanstalt. XXI. (1871), p. 297.

Neumayr, M. and **Uhlig, V.** Ueber Ammonitiden aus den Hilsbildungen Norddeutschlands. Palæontographica, XXVII. (1881), p. 135.

Newton, R. B. and **Harris, G. F.** British Eocene Cephalopoda. Proc. Malacol. Soc. I. (1894), p. 119.

Orbigny, A. d'. Paléontologie française. Terr. crét. I. 1840–41. Terr. jurassiques, I. 1842–49.

Phillips, J. British Belemnitidæ. 1865–1909. (Palæont. Soc.)

Pompeckj, J. F. Revision d. Ammoniten d. schwäbischen Jura. 1893, 1896.

Quenstedt, F. von. Die Ammoniten des schwäbischen Jura. 1883–89.

Schlüter, C. Cephalopoden der oberen deutschen Kreide. Palæontographica, XXI., XXIV., 1871–76.

Sharpe, D. Mollusca in the Chalk of England. Cephalopoda. 1853–4. (Palæont. Soc.)

Smith, J. P. Carbonif. Ammonoids. U. S. Geol Surv. Mon., 42. 1903.

Swinnerton, H. H. and **Trueman, A. E.** Morphology and development of the Ammonite Septum. Q. J. G. S., LXXIII. (1918), p. 26.

Wright, T. Lias Ammonites. 1878–86. (Palæont. Soc.)

Würtenberger, L. Über die Stammesgeschichte der Ammoniten. 1880.

Zittel, K. A. Die Cephalopoden der Stramberger Schichten. 1868.

ARTHROPODA

1. *Crustacea*

Ammon, L. von. Beitrag zur Kenntniss der fossilen Asseln. Sitz. d. kk. Akad. d. Wissensch. math.-phys. Classe. IV. (1882), p. 507.

Barrande, J. Système Silurien de la Bohême. Trilobites. 1852. Supplement 1872.

Bate, C. S. Crustacea Macroura (Challenger Report). 1888.

Beddard, F. E. Isopoda (Challenger Report). 1884, 1886.

Beecher, C. E. Structure and Development of Trilobites. 'Studies in Evolution' (1901), pp. 109–225. G. M. (1902), p. 152.

Bell, T. Fossil Malacostracous Crustacea of Great Britain. 1858–1913. (Palæont. Soc.)

Calman, W. T. Crustacea (Lankester's Zoology, VII. 3). 1909.

Darwin, C. (1) Fossil Lepadidæ. 1851. (2) Fossil Balanidæ. 1854. (Palæont. Soc.)

Edwards, H. Milne. Histoire naturelle des Crustacées, 1834–40.

Fritsch, A. See under *Arachnida*.

Hall, J. and **Clarke, J. M.** Trilobites and other Crustacea, Lower Palæozoic. (Geol. Survey of New York. Palæont. VII.) 1888.

Huxley, T. H. *Pygocephalus* from Coal. Q. J. G. S., XIII. (1857), p. 363.

Jones, T. R. (1) Fossil Estheriæ. 1862. (2) Tertiary Entomostraca. 1856, 1889. (3) Cretaceous Entomostraca. 1849, 1890. (Palæont. Soc.) (4) and **Woodward, H.** British Palæozoic Phyllocarida. 1888–92. (Palæont. Soc.)

Jones, T. R., Kirkby, J. W. and **Brady, G. S.** British Entomostraca from the Carboniferous. 1874–84. (Palæont. Soc.)

Lake, P. British Cambrian Trilobites. 1906– . (Palæont. Soc.)

Lapworth, C. *Olenellus callavei*. G. M. (1891), p. 529.

Lindström, G. Visual Organs of Trilobites. Kon. Svenska Vet. Akad. Handl., XXXIV. 1901.

Miers, E. J. Brachyura (Challenger Report). 1886.

Oppel, A. Ueber jurassische Crustaceen. (Palæont. Mittheil.) 1862.

Packard, A. S. N. American Phyllopod Crustacea. (Geol. Survey of the Territories 12th Ann. Rep.) 1883.

Peach, B. N. (1) *Olenellus* in N. W. Highlands. Q. J. G. S., XLVIII. (1892), p. 227; L. (1894), p. 661. (2) Higher Crustacea of the Carboniferous of Scotland. Mem. Geol. Surv., 1908.

Salter, J. W. British Trilobites. 1864–1883. (Palæont. Soc.)

Sars, G. O. Report on Phyllocarida (Challenger Report). 1887.

Smith, G. Anaspidacea. Q. J. Micr. Sci. LIII. (1909), p. 489.

Stebbing, T. R. R. Amphipoda (Challenger Report). 1888.

Vogdes, A. Bibliography of Palæozoic Crustacea. Ed. 2, 1893.

Walcott, C. D. (1) Fauna of the Lower Cambrian or Olenellus zone. (Ann. Rep. U. S. Geol. Survey.) 1890. (2) The Trilobite: New and Old Evidence. (Bull. Mus. Comp. Zool., VIII.) 1881. (3) Cambrian Geology and Palæontology. 4 vols. 1909–1918. (Smithson. Miscell. Coll. 53, 57, 64, 67.)

Withers, T. H. (1) Cretaceous and Tertiary Cirripedes referred to *Pollicipes*. A. M. N. H. (8), XIV. 1914, p. 167. (2) New Cirripede (*Proverruca*) from the Chalk. Proc. Zool. Soc., 1914, p. 945. (3) Palæozoic Cirripedia. G. M., 1915, p. 112.

Woodward, H. (1) Catalogue of British Fossil Crustacea. 1877.

(2) British Carboniferous Trilobites. 1883–4. (Palæont. Soc.) (3) *Pygocephalus*. G. M. (1907), p. 400. (4) *Præanaspides*. G. M. (1908), p. 385. (5) and **Salter.** Chart of Fossil Crustacea. 1865.

2. *Myriapoda*

Peach, B. N. Myriapods from the Old Red Sandstone of Forfarshire. Proc. Roy. Phys. Soc. Edin. VII. (1882), p. 77; XIV. (1899), p. 113.

Scudder, S. H. (1) Archipolypoda, a type of Carboniferous Myriapods. Mem. Boston Soc. Nat. Hist. III. (1882), p. 143. (2) Two new types of Carboniferous Myriapods, *ibid.* III. (1884), p. 285.

Woodward, H. Carboniferous Myriapods. G. M. (1887), p. 1.

3. *Insecta*

Brodie, P. B. Insects in the Secondary rocks of England. 1845.

Brongniart, C. L'histoire des Insectes des Temps Primaires. Bull. Soc. Industr. Min. St Étienne. Sér. 3, VII. 1893.

Handlirsch, A. (1) Die fossilen Insekten und die Phylogenie der rezenten Formen. 1906. (2) Revision of American Palæozoic Insects. Proc. U. S. Nat. Mus. XXIX. (1906), p. 661.

Scudder, S. H. (1) Index to the Fossil Insects, including Myriapods and Arachnids. Bull. U. S. Geol. Survey, 1891. (2) Bibliography of Fossil Insects, *ibid.* 1890. (3) Palæodictyoptera. Mem. Boston Soc. Nat. Hist. III. (1885), p. 319. (4) Fossil Insects of North America. 1890.

4. *Arachnida*

Fritsch, A. (1) Fauna der Gaskohle, etc. IV. 1901. (2) Palæozoische Arachniden. 1904.

Holm, G. *Eurypterus.* Mém. Acad. impér. Sci. St Pétersbourg (8), VIII. 1898.

Huxley, T. H. and **Salter, J. W.** *Pterygotus.* (Mem. Geol. Survey, Organic Remains.) 1859.

Laurie, M. Eurypterida. Trans. Roy. Soc. Edinburgh, XXXVII. (1892), p. 151, (1893), p. 509; XXXIX. (1899), p. 575.

Peach, B. N. Scorpions from the Carboniferous of Scotland and the English Borders. Trans. Roy. Soc. Edin. XXX. (1881), p. 397, (1882), p. 511.

Pocock, R. I. Silurian Scorpion. Q. J. Micr. Sci. XLIV. (1901), p. 291.

Schmidt, F. Die Crustaceenfauna der Eurypterusschichten von Rootziküll. Mém. Acad. impér. St Pétersb. (7), XXXI. (1883), p. 28.

Woodward, H. (1) The Xiphosura. Q. J. G. S. XXIII. (1867), p. 28; XXVIII. (1872), p. 46. (2) The Merostomata. 1866–78. (Palæont. Soc.)

INDEX

Names of genera are printed in italics

CAMBRIDGE: PRINTED BY J. B. PEACE, M.A., AT THE UNIVERSITY PRESS